The ESSENTIALS OF PLANT BIOLOGY

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PREFACE

A scholarly President of the United States once said that he was materially opposed to systematic writing, "because no man knows enough about anything to write about it systematically." He said that no man knows more about a certain subject than some parts. When starting to write systematically, he pointed out, there must be some sort of plan, a table of contents, a systematic scheme of chapters. "Some contain things he knows; some contain things he doesn't know, but has taken from somebody else; and he fixes the surface so that all will look alike, the parts not being divided," said the President.

A book about the essentials of plant biology must be written systematically, whether or no. The pattern of content and its form of presentation must be given first consideration. The plan of this book has been developed in an attempt to portray the unity of plant life—the maintenance of individual life in Part I and the preservation of racial life in Part II. The topics and materials are those in current use, the development of interest being uppermost in determining their sequence and integration. It has been my intent to make a functional approach, but to be consistent is difficult.

I had thought not to mention objectives, indispensable as they are, but I cannot forgo saying that some things have been included to emphasize certain aspects of plant science that enter into daily life; and others, to develop reflective concepts that have a bearing on human culture and progress.

I am indebted to my associates at The Pennsylvania State College for their help and cooperation in the preparation of this volume. Special thanks are due Dr. C. C. Wernham, who joined me in writing the manuscript for Chapter 12; Dr. H. W. Thurston for his aid with the proofs; Dr. J. Ben Hill for many valuable suggestions; and Miss Grace Thomas for assistance in the preparation of the index. One of my greatest obligations is to my good friend, Dr. Harold H. Clum of Hunter College, for his critical reading of the manuscript.

The illustrations include numerous photomicrographs. It has been found that they aid materially in establishing certain concepts. I have in-

cluded also many diagrams. These supplement the more conventional type of photographs and drawings. The illustrations that are not original have been obtained from various sources. I am particularly indebted to Dr. George H. Conant, Triarch Botanical Products, for making possible the inclusion of two photomicrographs in color. Mr. Philip Bonhag made many of the new drawings; Miss Louise Burpo contributed several; Dr. L. O. Overholts, Dr. D. A. Kribs, and Mr. Homer Grove assisted me with the preparation of numerous photographs. I make my grateful acknowledgment to all who have aided me.

It is impossible to name individually the many biologists whose work makes possible the presentation of such a book as this; it must be recognized that to them the real credit is due.

FRANK D. KERN

State College, Pennsylvania
August, 1947

INTRODUCTION

Through the centuries of civilization man has relied upon plants for many of life's requirements. After ages of progress in ways of living we are more rather than less dependent upon plants as the ultimate sources of many necessary products. We use them for food, fuel, shelter, clothing, and medicines. We depend also upon plants for making our homes and surroundings habitable, healthful, and attractive. Plants furnish both necessities which make our existence possible and accessories which make our lives pleasurable. To come to an appreciation of the service of plants to mankind, we must make an effort to understand how plants live, develop, and reproduce; how they are being improved; and how their products are being more widely and effectively used. Plant biology, or botany, deals with these topics.

Some persons study medicine to become physicians, others study law to become attorneys. The world needs these practitioners, but we are also aware that a general knowledge of the fundamental principles of these professions is a great asset to all of us. Likewise, professional botanists must carry on the work and development of plant science, but we cannot escape the fact that the life of no one can be complete, nor any education liberal, without a realization of the significance of plants in human affairs. Someone has truly said that man would rapidly come to such a realization if some mysterious catastrophe were suddenly to annihilate all plant life. Fortunately such a method is not necessary. Through study and observation it is possible to come to an understanding of plants, their forms, their uses, their habits, their ways of nutrition, reproduction, and adjustment to surroundings. Only with such knowledge will come an appreciation of man's efforts to utilize the wealth of plant life and a realization of the possibilities of yet undiscovered utilities. Even to be able to comprehend many references in papers, magazines, and books, we must have some knowledge of plant biology.

THE PLANT BODY

For the past hundred years there has been an increasing tendency to liken a plant to a mechanism "having specialized parts which perform the vari-

ous functions upon which the maintenance of its life depends." It must be understood that a reference to a plant as a machine is made in a figurative and not in a literal sense. A machine does not build, repair, or reproduce itself. A plant does all these things and thus is fundamentally different.

We shall do well to begin our studies by obtaining a general plan of the structure of the body of ordinary seed plants (Fig. Introd.–1). Roots, stems,

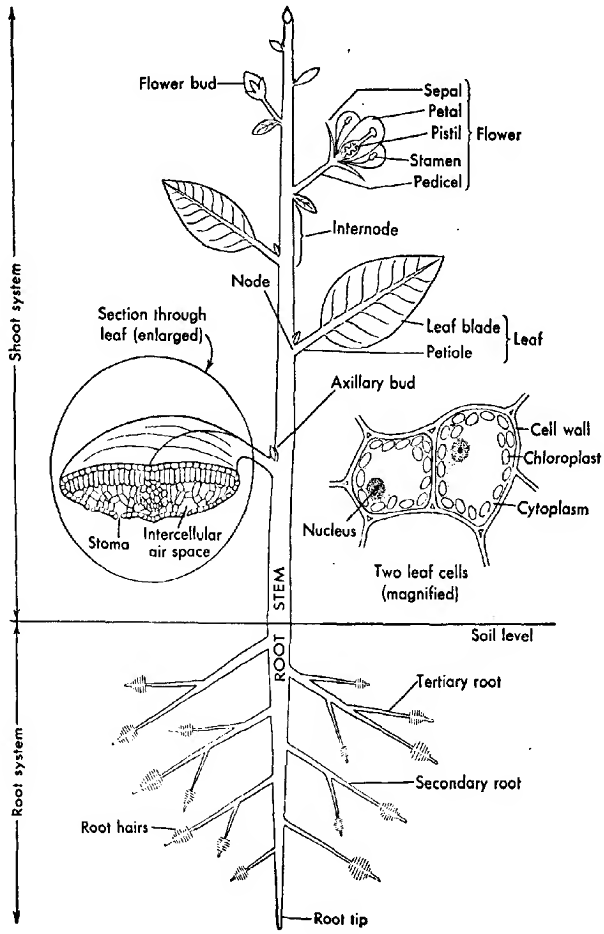


Fig. Introd.–1. Organization of a seed plant (Diagrammatic).

leaves, flowers, fruits, and seeds are familiar objects. From past experiences most people have formed general ideas of these several parts of plants. In order to understand the inner working of a living plant it is necessary to expand somewhat these general ideas of the grosser features and relations of the different parts and also to learn something of the minute structure as well.

Plants show a great variation in the form, arrangement, and development of their parts and yet the general plan is rather uniform. There are two principal working parts, root system and shoot system. We refer to these systems as the working parts because they carry on the life processes of the individual; botanically they are known as the vegetative organs. These life processes include the absorption of materials, their distribution and use, and the provision of energy for growth and development. Flowers are concerned with the perpetuation of the race through the formation and dispersal of seeds from which new plants arise; they are reproductive organs. Not all plants produce flowers. Ferns are without flowers and their reproduction does not take place through seeds, but by other special reproductive structures known as spores. The algae and fungi are other flowerless plants reproducing by spores. Their working bodies are also different in not having roots, stems, or leaves.

For the present, however, let us consider the body of a seed plant. The usual root system grows beneath the surface of the ground, serves to anchor the plant firmly in the soil and to withdraw from it water and dissolved substances, which form part of the raw materials used in growth. Roots conduct the absorbed water and dissolved substances upward into the shoot system and receive other substances from the shoots. Under the term shoot system a stem and its leaves are collectively included. The shoot system normally extends above the ground as a continuation of the root system and often grows extensively both upwards and outwards. The stems bear and support the leaves, flowers, and fruits, and conduct materials from roots to leaves and from leaves to roots. The majority of leaves are flat green structures. The green leaves are essentially the food-making organs of the plant. The veins, which are usually evident in leaves, serve as a supporting framework and also as conductors of materials both to and from the leaf.

Having in mind the general plan of the grosser construction of the body of a plant, we should endeavor to obtain next some concepts of the more minute structural features. These ideas and concepts may seem vague at first, but they will be useful for reading, discussion, and observation, and they gradually will become expanded and more adequate.

If parts of the body of a plant are examined with the aid of a microscope they are found to have a honeycomb appearance. The individual structural units are called *cells.* The cells vary in size in the different organs of the plant body, but a general idea of their minuteness is gained from the fact that there are about 50,000,000 of them in an ordinary apple leaf. Many plant cells are more or less box-like structures. The early workers with the microscope saw the framework, or walls, of the cells and were much impressed by them. Later it became evident that life was inherent in a substance within the cells which came to be called *protoplasm,* and that the walls are a product of its activity. The protoplasm is almost universally divided into two portions, an outer colorless jelly-like mass (*cytoplasm*) enclosing a denser globule (*nucleus*). The *cytoplasm* commonly surrounds cavities (*vacuoles*) which are filled with watery solutions (*cell sap*), one or more protoplasmic bodies (*plastids*), and also non-protoplasmic particles (*food granules*) which give it a grayish granular appearance.

Cells are arranged in groups called tissues. A plant tissue may be composed of living cells, or of dead cells, or of both living and dead cells. The cells vary greatly in shape and structure in the different tissues. In the conducting tissues they are elongated and narrow; in supporting tissues they have thick strong walls; in growth tissues at the tips of roots or stems they have thin walls and abundant protoplasmic contents. There are many kinds of tissues and there is a correlation of structural features with the different functions.

The bodies of all plants, and animals too, grow and develop through the formation of new cells by division of preexisting cells. The living body is composed of organized protoplasm and its products. It is important to think of cells as component structural units of the body but it is also important to realize that they have functional relations to the activities of the individual organism of which they are parts. There is an interdependent relation between the cell units and the organism as a living being—the parts affect the whole and the whole affects the parts.

THE STUDY OF PLANTS

The field of biological study is extensive; the science of *biology* includes all knowledge of plants or of animals or of both. The facts and principles of biology are commonly separated into those pertaining to plants, called *botany,* and those pertaining to animals, *zoology.*

Because there are so many different kinds of plants and their life rela-

tions are so varied and complex, there have been developed within the science of botany a number of specialized divisions, such as *taxonomy,* dealing with names, description, and systematic classification; *physiology,* the study of the processes and reactions which go on in the living body; *morphology,* concerned with the form and structure of parts, and their relationships to one another; *pathology,* which is a consideration of diseases; *ecology,* which explains the relations between plants and their environment; *genetics,* the study of heredity; and *cytology,* which deals with the structural and functional organization of protoplasm. A broad study of plant life involves some consideration of all these interacting phases of biology and requires also a general background of physical and chemical knowledge.

We cannot proceed very far with the study of plants without using names for them, or without referring to them as groups. It will be well, therefore, to learn some of the basic facts about plant names and classification early in our studies.

Many plants have common names. They are much used and serve a useful purpose, but they have their limitations. They lack definiteness and cannot be used satisfactorily in different languages. Botanists use Latin names which can be internationally applied. In applying common names to plants we recognize the fact that they fall into groups according to the degrees of their likenesses. We speak of the oaks, the maples, the roses, and the buttercups. The trees that we call oaks are not all alike; hence we refer to some of the different kinds as white oaks, red oaks, or black oaks. Botanically the name of the oak group, or *genus* as it is called, is *Quercus;* the different kinds, or *species,* must have two names, e.g., white oak, *Quercus alba,* red oak, *Quercus rubra,* and black oak, *Quercus nigra.* Similar individuals constitute a species; groups of species which resemble one another more or less closely form a genus. When one Latin name is used alone it is always the genus name. In detailed schemes of classification many larger groups are successively established.

To some of these large groups we have already referred; a further description, even though brief, will be helpful, with other references which will come later. The *fungi* are non-green plants including such groups as the yeasts, molds, mushrooms, and toadstools. The *algae* are seedless plants, comprising especially pond scums and seaweeds. The *liverworts* and *mosses* are small, seedless plants, occurring typically as a ground cover in the woods. They may have a leafy shoot but do not have roots. The *ferns* are larger, seedless plants, best developed as undergrowth in the forest shade. They

have shoots and roots. The *seed plants* constitute the largest and most widely known group. In the majority of them seeds are produced through the development of flowers and fruits. (See Figs. Introd.–2 and 3.)

In brief outline we have sketched the body of a green, leafy, seed plant and we have said a word about other kinds of plants. These general con-

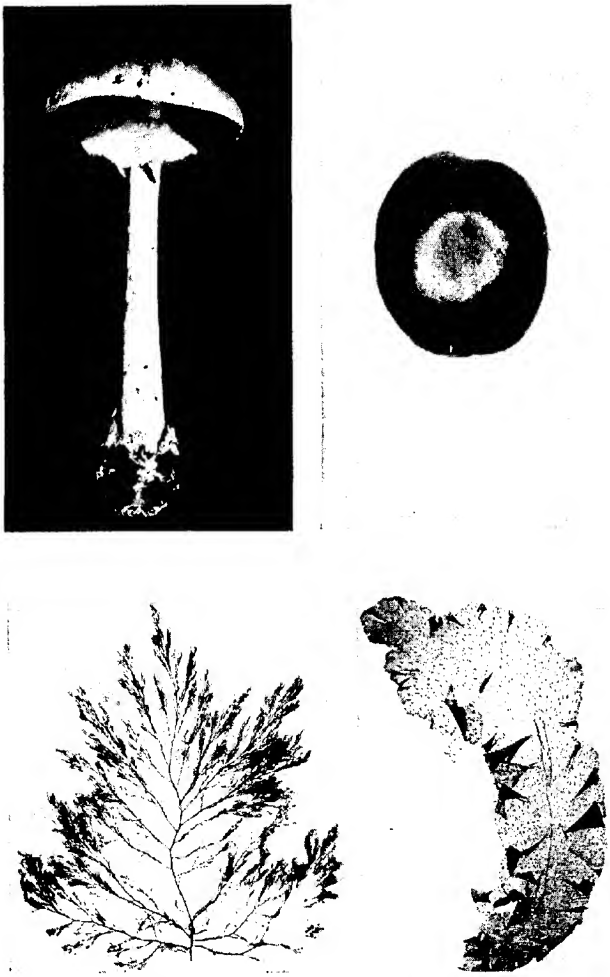


FIG. Introd.–2. Fungi (above) and red algae (below).

siderations of form; of organs, tissues, cells, and protoplasm; and of classification, are a prelude to the main biological considerations which follow. The highest aim must be a unified view of functions and forms. Plants are our inheritance from nature, and the importance of studying them has

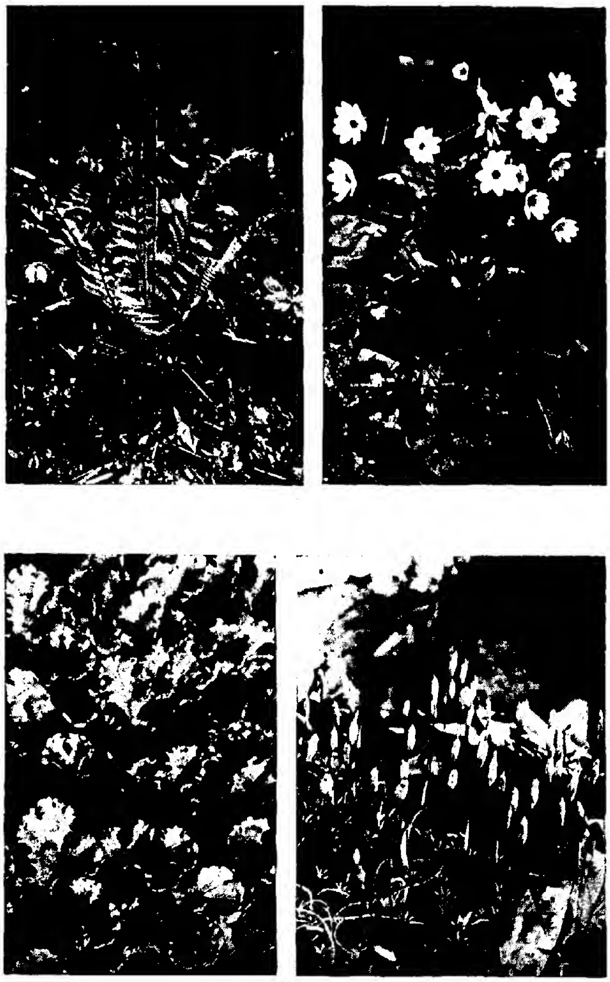


FIG. Introd.-3. A fern; a flowering plant; a liverwort; a moss.

long been recognized. Everyone can come to an appreciation of what man has done toward conquering and utilizing the plant world. Those who wish to go further will find that the conquest is incomplete; there are still many interesting and unsolved problems, many rich opportunities for original research work.

PART I

THE MANIFESTATION OF LIFE

(Individual Maintenance)

CHAPTER 1

THE FOOD SUPPLY OF PLANTS

(Nutrition)

It is a well-appreciated fact that animals must have food to sustain life. It is equally true of plants but not equally well appreciated. Animals move about and many times their movements are associated directly with a search for food. Plants remain rooted to a spot. Animals, at least many of them, feed in such a way that we are well aware of their intake of food. We do not see plants take anything into their bodies.

But plants grow and this may be taken as indirect evidence of their nourishment. Since plants do not move, we would seem to be justified in concluding that their food comes to them. This is not quite true, but it is true that raw materials come to them from the air and the soil, and the plants construct their food from these raw materials inside their own bodies. In these general statements we are referring to green plants and not to parasites or other non-green plants, such as mushrooms, toadstools, and puffballs.

It should be understood that the term *food* may be defined and used in a broader sense than we have determined to use it. We have just said that the inorganic substances which enter the plant from the soil are not food. Practical agriculturists, however, usually speak of fertilizers as plant foods. Many scientific agriculturists also adopt this usage. They say that soils lack certain plant foods and that these need to be added in order that the plants may grow well. What they add are inorganic salts or unavailable organic materials which are converted in the soil into available inorganic compounds. Such a conception of food is not without support among biologists. It can be held, also, that the term food must be broad enough to include mineral constituents because they are found in the living substance of the body called protoplasm. However, in this discussion these things are not to be considered as foods. For our purposes the term food includes only organic substances (we call them carbohydrates, fats, and proteins). The term nutrition is used to include all the processes by which food is secured or transformed.

The first step in the natural production of foods is known as photosynthesis. The term means "putting together in the light" and is an appropriate one because the process takes place only in the light. Under the influence of the green coloring matter, chlorophyll, the living plant combines the elements carbon, hydrogen, and oxygen, of the compounds carbon dioxide and water, to form carbohydrates. In this process the free energy of light is stored. These carbohydrate foods, better known as sugar and starch, may be used as such, or they may be used as the basis for the synthesis of fats and proteins. For protein synthesis there are used also several minerals such as nitrates, sulphates, and phosphates which plants absorb from the soil.

PHOTOSYNTHESIS

Photosynthesis is a factor of such importance in life, not only for plants but also for animals and man, that an attempt to learn more about the process and the conditions under which it is carried on is incumbent on the student of biology. The great majority of living organisms, both plants and animals, depend upon the process and products of photosynthesis to sustain life. There are some plants, such as the fungi, which cannot carry on photosynthesis and hence are also dependent directly or indirectly upon the plants which are independent through photosynthesis. Some kinds of bacteria manufacture their own food by another process; these organisms are not dependent upon the photosynthetic process for their food supply. With these exceptions, the process of photosynthesis furnishes the food for the entire living world. Of equal significance is the fact that photosynthesis is the means by which the supply of atmospheric oxygen, upon which all life depends, is replenished (see Fig. 2–10).

Photosynthesis is of broader benefit to man than in the supplying of food. Photosynthesis is an energy-storing process of great importance. The radiant energy of sunlight is transformed by the green plants to potential energy in sugar. For every gram of sugar made, 3.75 calories of light energy are transformed to chemically bound energy. Most of the energy that man uses in the form of heat, electricity, and mechanical power can be traced to plants. The potential energy of fuel, whether wood, coal, or oil, is sunlight stored in photosynthesis.

Relation Between Chlorophyll and Photosynthesis

Reference has been made to the fact that green plants are the ones in which the process of photosynthesis is carried on. If the entire plant body

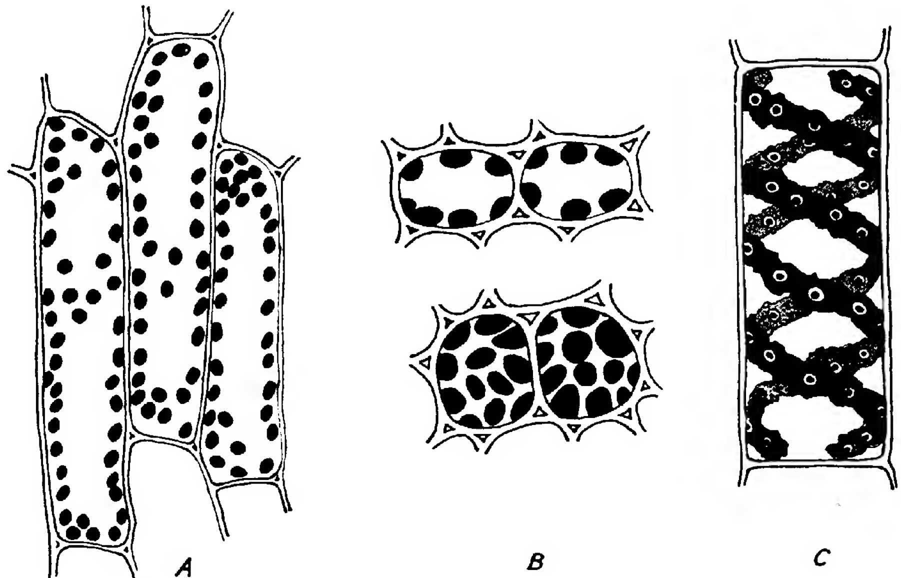


FIG. 1-1. Structure and distribution of chloroplasts. *A*, in cells of ditchmoss (*Elodea*); *B*, in cells of a moss (*Atrichum*)—above in strong light, below in light of diminished intensity (after Schimper); *C*, spiral band-like chloroplasts in a pond scum (*Spirogyra*).

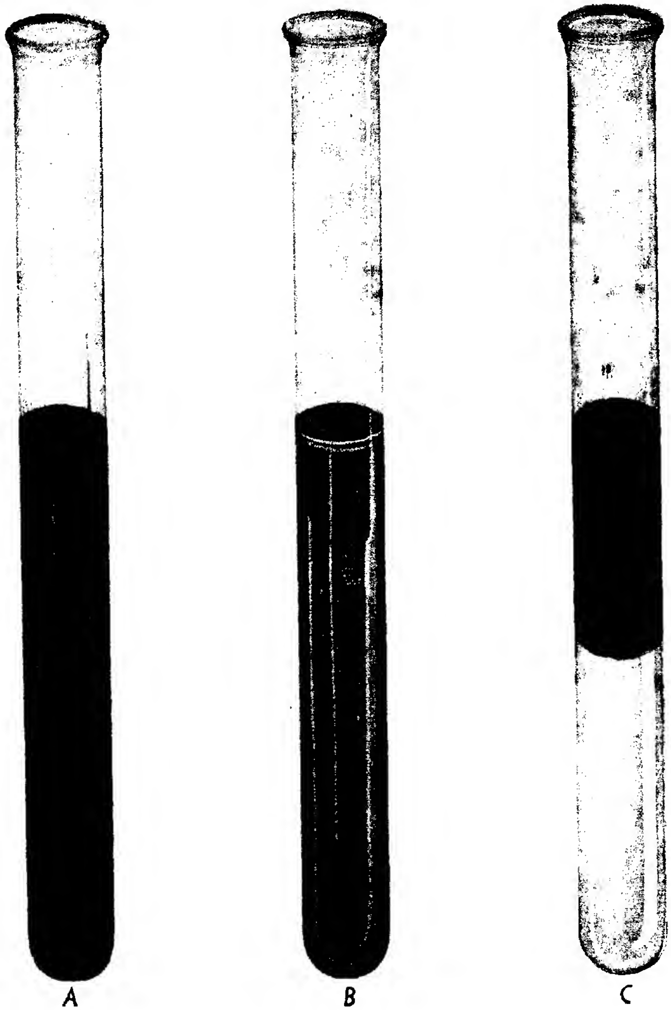


FIG. 1-2. Chlorophyll extracts in test tubes. *A*, alcoholic extract; *B*, the same after exposure to sunlight; *C*, alcoholic extract to which benzene has been added (see text for further explanation).

is not green, then it is only in the green parts, such as the leaves or green stems, that there is photosynthetic activity. The green color in plants is due to the presence of two green pigments, properly designated *chlorophyll a* and *chlorophyll b,* but usually referred to by the one term chlorophyll. Although a leaf looks green as if the green pigment were present throughout the whole material structure, this is not the case. A microscopic examination reveals the presence of the chlorophyll only in small dense protoplasmic bodies or *plastids,* called *chloroplasts,* embedded in the more fluid protoplasm or cytoplasm of the cells (Fig. 1–1). The shape, size, and distribution of these chloroplasts may vary in different kinds of plants, but they are commonly roundish or lens-shaped, very small, and lie in the protoplasm close to the cell wall. (In a way the plastid and the green pigments are independent of each other and yet they are not.)

Certain plants sometimes produce chlorophyll in darkness. Potatoes sprouting in a dark cellar grow long yellowish shoots. If a board lies on the grass for a while the grass loses its green color. In these cases the plastids are present but the green pigment is not. Light is necessary for the formation and existence of the chlorophyll. If a seed is germinated in total darkness the shoot does not develop chlorophyll. If living green plants are put into darkness and kept there they will gradually lose the chlorophyll which had been present. The blanching of celery is a good example of the loss of chlorophyll.

We can separate the chlorophyll pigments from the plastids by soaking green plant tissues in certain chemicals which will dissolve the chlorophyll. Chloroform, ether, benzene, acetone, and alcohol will serve the purpose. Common grain alcohol is most often used for laboratory experiments, and if heat is applied the extraction is hastened. Chlorophyll does not dissolve in water even if green leaves are boiled in it.

It can be shown readily that the alcoholic extract is not a simple compound. If benzene is poured slowly into a test tube partly filled with an alcoholic extract, and a few drops of water are added, there will be a separation (Fig. 1–2). The benzene will rise to the top and will be bluish-green, while the alcohol which remains below will be yellow. Chemical analysis has revealed that there are two pigments in the benzene, *chlorophyll a* and *chlorophyll b;* the former is blue-green and the latter yellow-green. The chlorophyll *a* and *b* are definite compounds and are always present in all green plants. The yellow color in the alcohol is due to pigments known as *carotenoids.* They are always associated with the chlorophyll in green tissues. They also occur in roots, flowers, and fruits in the absence of chlorophyll. They are the cause of the yellow color of carrots,

sunflowers, lemons, and oranges. The carotenoids are responsible for the yellow color of animal body fat, butter fat, and egg yolks. One of the carotenoid pigments (β carotene) is converted into vitamin A in the animal body.

There are two other facts about the alcoholic extract which can be discovered without difficulty. It is fluorescent, i.e., it looks green by transmitted light and reddish or brownish by reflected light. If some of the extract is divided between two tubes and one of them is exposed to sunlight for a short time, the other being kept in the dark, it will soon be evident that the one in the light has changed to a muddy brownish color, whereas the tube in the dark is unchanged. Light has broken down the green pigments. A similar destruction doubtless occurs in the living green tissues in the light, but so long as the formation equals the destruction they do not appear to change. Under the unfavorable conditions of the autumn, which prevent the formation of new chlorophyll, the green color does disappear and yellow and red colors prevail. The yellow color is due to the carotene pigments which were present but masked, and the red is due to the development of other pigments (*anthocyanins*) which were not present previously. The red pigments appear in the cell sap and are soluble in water. In some plants, such as coleus and red cabbage, the red pigments are present throughout the growing season and mask the green pigments which are also present. In some bacteria there is present a purple pigment which is chlorophyll-like and enables them to carry on photosynthesis. These plants which appear red or purple are exceptions to the general statement that only green plants carry on photosynthesis.

The first product of the photosynthetic process is a soluble sugar known as glucose, but in many plants this sugar is very quickly changed into starch. Food in the form of starch is insoluble in cold water. In the cells it exists as grains, easily visible with a microscope. The form and size of the grains vary in different plants (Fig. 1–3). Food analysts are often aided in their work by the identity of starch grains which they can determine by microscopic examination. At night the starch is changed back to sugar and is removed from the working cells and transported through the veins of the leaves to the stems and other parts of the plant body. Not all of the starch, however, may be removed from the green leaves during only one night. The rapidity of transportation varies in different kinds of plants and may vary in the same plant at different stages of development.

Since iodine turns starch a blue color it is possible to use it as a test for the presence of starch. In order that the blue color may show, green leaves

are first blanched by heating them in alcohol. When iodine is added to such whitened leaves not only can we detect the presence or absence of starch but by the depth of the blue color we can get a general idea of the amount of starch present. Tests have shown that young plants of sunflower, castor bean, common bean, and cabbage will remove all the starch from their leaves in one night. The common geranium must be kept in the dark two nights and one day (and corn three nights and two days) before all traces of starch are removed from the leaves.

In order to experiment with the manufacture of starch, the experimental plants should be placed in the dark long enough to drain them of their starch. They should not, however, be kept in the dark longer than necessary since that might cause the chlorophyll to break down.

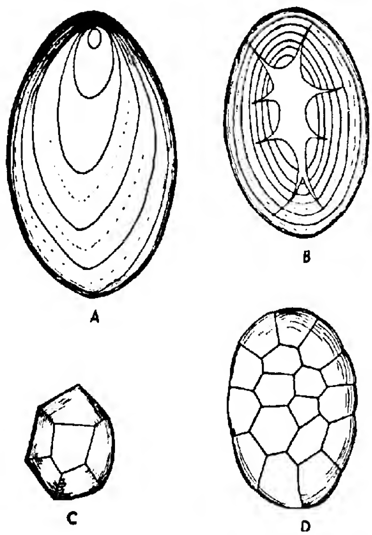


FIG. 1–3. Grains of four different kinds of starches. *A*, potato; *B*, bean; *C*, corn; *D*, oats.

One of our first experiments may be to determine whether chlorophyll is really responsible for the food-making process. A potted plant of some species which has variegated leaves supplies the material for the test. One of the geraniums used for borders of flower beds, sold under the trade name of Mme. Saleroi, is an excellent plant for this purpose. Chlorophyll is present only in the centers, there being a well-defined white margin to practically every leaf. If we take these leaves from plants that have been destarched by keeping them in the dark, remove the chlorophyll by heating in alcohol, and apply iodine, we will of course find no starch. Now if the plant is left in the light for an hour or even less and if leaves are then tested in the same manner, we find starch present in the center distributed exactly in the same area where the cholorophyll was located. There is no blue color in the white margin where the chlorophyll was lacking. Here is evidence that chlorophyll is necessary for photosynthesis (Fig. 1–4).

Relation Between the Raw Materials and Photosynthesis

The chemists tell us that the formula for the sugar, glucose, is $C_6H_{12}O_6$. Such a compound can be formed from CO_2 (*carbon dioxide*) and H_2O (*water*) with an excess of O_2 (*oxygen*) according to the following equation:

$$\text{Energy} + 6\,CO_2 + 6\,H_2O = C_6H_{12}O_6 + 6\,O_2$$

Starch originates from the glucose ($C_6H_{12}O_6$) by transformation. The formula is $(C_6H_{10}O_5)_n$. This means that there is a loss of water and that the combination $C_6H_{10}O_5$ is repeated an unknown number of times in the molecule.

While the above equation showing how carbon dioxide and water may be combined to form glucose looks simple, the actual process in the plant

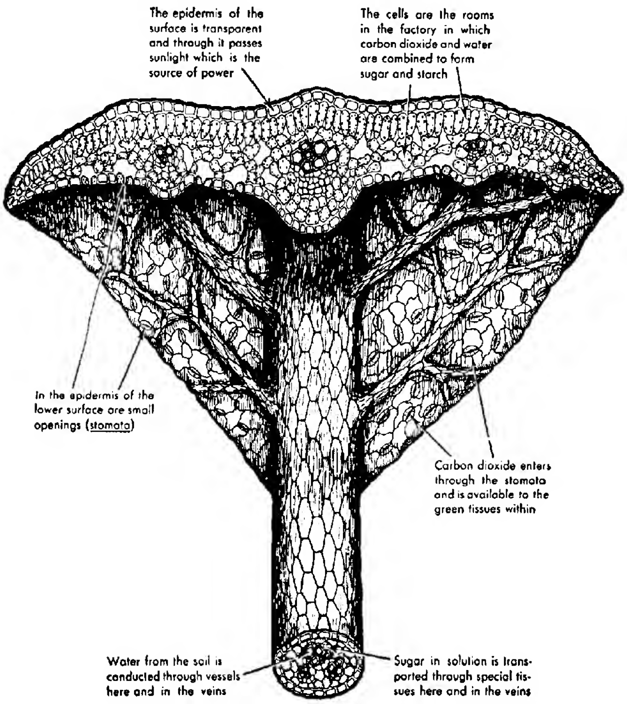


FIG. 1–5. A green-leaf photosynthetic factory. (Drawing by Louise Burpo.)

FIG. 1-4. Experiment showing the necessity of chlorophyll for photosynthesis. *A*, fresh leaf of a variegated geranium; *B*, the same leaf with the chlorophyll extracted and treated with iodine. Note that the starch pattern corresponds with the chlorophyll pattern in *A*.

is not simple. There is every reason to believe that the process is extremely complex. There has been much chemical and physiological investigation of the process of photosynthesis.

These facts are well established: (1) Chlorophyll and light are necessary; (2) carbon dioxide and water are the raw materials; (3) carbohydrates are formed and oxygen is liberated (Fig. 1–5). It is certain that for every volume of carbon dioxide used, an equal volume of oxygen is liberated. Although many theories have been advanced, the chemical reactions suggested for transforming the raw materials into the products (carbohydrates and oxygen) must be considered speculative. One of the recent theories is that chlorophyll actually combines with carbon dioxide and water as a first step; then there occurs a molecular rearrangement resulting in a complex compound of the nature of a peroxide. The carbon of this compound which originally came from the carbon dioxide is then reduced, possibly by a shift of hydrogen atoms from water to another chlorophyll molecule and then to the carbon, and glucose is eventually formed, probably with the aid of enzymes (substances manufactured by living protoplasm and effecting chemical changes). According to this theory, only the intermediate reaction is photochemical, the first and last reactions being purely chemical. This theory also makes chlorophyll play a larger part than absorbing light since it assumes that the chlorophyll combines chemically with the raw materials.

That carbon dioxide is necessary for photosynthesis is a fact which can be proved readily. The gas, when present in the air, enters the leaves through small openings (stomata) in the layer of surface cells (epidermis). Green leaves in an atmosphere devoid of carbon dioxide do not show any starch reaction. The results are conclusive. For the test (Fig 1–6), a gallon bottle with a fairly wide neck is used.

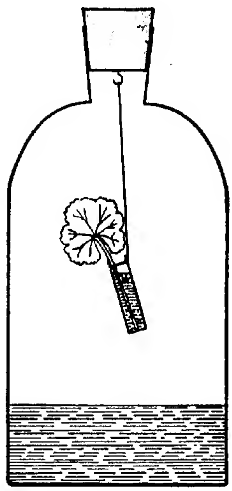


Fig. 1–6. Method of suspending a leaf in an atmosphere devoid of carbon dioxide. See text for explanation.

From a rubber stopper there is suspended by a wire a small vial in which a detached leaf may be placed in water to keep it fresh. In the bottom of the bottle is placed a solution of potassium hydroxide. This absorbs the atmospheric carbon dioxide so that the leaf suspended in the vial has no

supply of the gas. A second bottle is arranged in exactly the same manner, except that water which does not absorb the carbon dioxide is placed in the bottom of the bottle instead of potassium hydroxide. The leaves for both bottles are taken from the same plant, which was previously kept in the dark in order to make certain that the leaves will be starchless at the beginning of the experiment. If the two bottles are exposed to sunlight for an hour, or even less, and the leaves then blanched in alcohol and tested for starch, the leaf from the bottle with water gives a positive reaction and the leaf from the bottle with potassium hydroxide gives a negative reaction.

The discovery, made about the end of the 18th century, that the carbon in plants comes from the carbon dioxide of the air ranks as one of the important milestones in the progress of the natural sciences. It was by no means easy to come to the conclusion that an element making up half the dry weight of plants had such an origin. It was much easier to believe that the carbon and all the other nutrient substances were taken up by the roots from the soil.

It is not so easy to prove the necessity of water for photosynthesis. Since water is always present in the cell sap it would be difficult, if not impossible, to set up an experiment in which water was lacking. Only if the supply of water is so low as to cause wilting is the process of photosynthesis affected.

Relation Between Light and Photosynthesis

The placing of two plants in the dark until all the starch is translocated from the leaves and the keeping of one there while the other is exposed to light is a simple test to prove the necessity of light for the process of photosynthesis, although all the other factors are present.

By placing a screen over a portion of a destarched leaf (Fig. 1–7) it can be shown that light must fall directly upon the green tissue in order to have photosynthetic activity. A piece of tin foil placed over part of the surface will be found to prevent starch formation in the area beneath it.

It is a well-known fact that the rays emanating from the sun are not a simple form of energy. There is a distribution of rays from the infra-red through visible light to the ultraviolet. Ordinary light is a combination of the rays of the spectrum which are visible. But not all the rays of the visible spectrum are equally effective. Studies have shown that the red rays are most active and that the blue-violet rays are of next importance (Fig. 1–8). Of the total amount of light energy falling upon plants, it is estimated that only about 1 per cent is used in the process of photosynthesis. How-

ever inefficient this may seem to make plants as agents for the storing of energy, we must keep before us the fact that they supply in this way all the energy for themselves, for animals, and for man. The storing of radiant energy is the most important part of the process of photosynthesis.

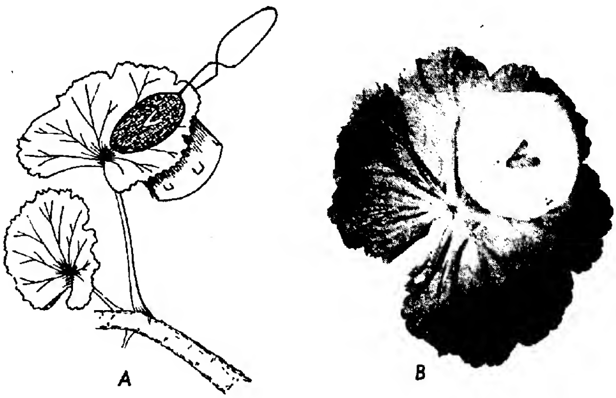


FIG. 1-7. Experiment showing effect of darkening an area of a green leaf by a light screen. The white of the darkened starchless area is in contrast to the blue of the areas exposed to the light. *A*, sketch to show method of applying screen; *B*, photograph showing result.

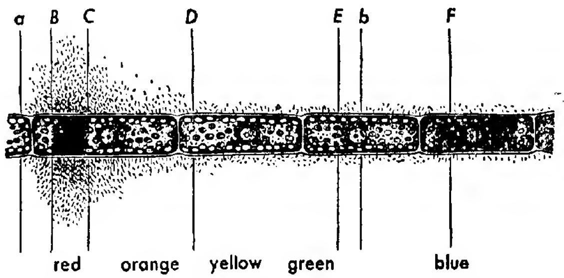


FIG. 1-8. Experiment showing the influence of the different rays of the spectrum on photosynthesis by throwing a spectrum on an algal filament. Since oxygen is liberated in photosynthesis the rate of photosynthesis may be estimated by the evolution of oxygen. Bacteria seek oxygen and are used as a test for its evolution. The greatest accumulation of bacteria is between *B* and *C*, the red region of the spectrum. (Adapted from Pfeffer.)

Conditions Affecting the Rate of Photosynthesis

It is estimated that the average rate of photosynthesis is about 1 gram of carbohydrate per square meter of leaf surface per hour. There are certain conditions which affect the rate in a very definite way.

One of the most important conditions affecting the rate of photosynthesis is the amount of carbon dioxide in the air. There are different sources of atmospheric carbon dioxide. It is released into the air by the respiration of plants and animals; from volcanoes and mineral springs; in the burning of coal, wood, and other fuels; and from the waters of the oceans and lakes. Ordinarily the percentage of carbon dioxide is rather uniform and very small—three-hundredths of 1 per cent, or 3 parts in 10,000. Carefully controlled experiments have shown that most plants increase the rate of photosynthesis perceptibly if furnished a larger supply. (The fact that plants can use a much higher percentage of carbon dioxide than is ordinarily present in the air is interesting.) Most common plants will respond to 20 to 30 times the usual concentration. This furnishes some grounds for believing that a larger percentage of carbon dioxide may have been present in certain geological ages, thus accounting for the luxuriant growth of plants at those times and also for the higher capacity of present-day plants. When the plant is artificially supplied with additional amounts, the increased rate of photosynthesis is soon evidenced by more rapid growth. It is very interesting to see the striking differences in growth between plants supplied with additional carbon dioxide and those grown in ordinary air, when all other conditions are kept constant.

Light affects the rate of photosynthesis, and unlike the supply of carbon dioxide light varies greatly in nature. It varies as to quality, intensity, and duration; and each of these factors may affect the rate of photosynthesis.

The relation between light and chlorophyll is very intimate. Light is necessary for the formation of chlorophyll, it is necessary for its activity, and at the same time it destroys chlorophyll. With these facts in mind it will not seem strange that light conditions are extremely important for the life and health of green plants.

Most plants flourish best in diffuse light. It is possible for the intensity of light to be too great. Different kinds of plants vary in their reaction to light intensity. Some plants can have noontime daylight reduced to 1/12 of its intensity before a decrease in photosynthetic activity occurs. Plants which endure shade can carry on some photosynthetic activity with low intensity. The Norway maple is capable of functioning when the intensity is 1/55 of noon daylight. The cherry, on the other hand, can stand a reduction of only 1/3 without interference with the rate of activity.

The daily duration of light may have an effect upon the growth of plants, particularly upon the development of flowers and fruits (Fig. 1–9). Many plants "attain the flowering stage only when the length of day falls within certain limits," some responding to short days and some to long days. These responses are attributable not to the effect of the quantity of light upon

food-making but rather to the number of hours. Other physiological processes may also be involved. Further reference to the influence of length of day is to be found in a later chapter where growth is discussed.

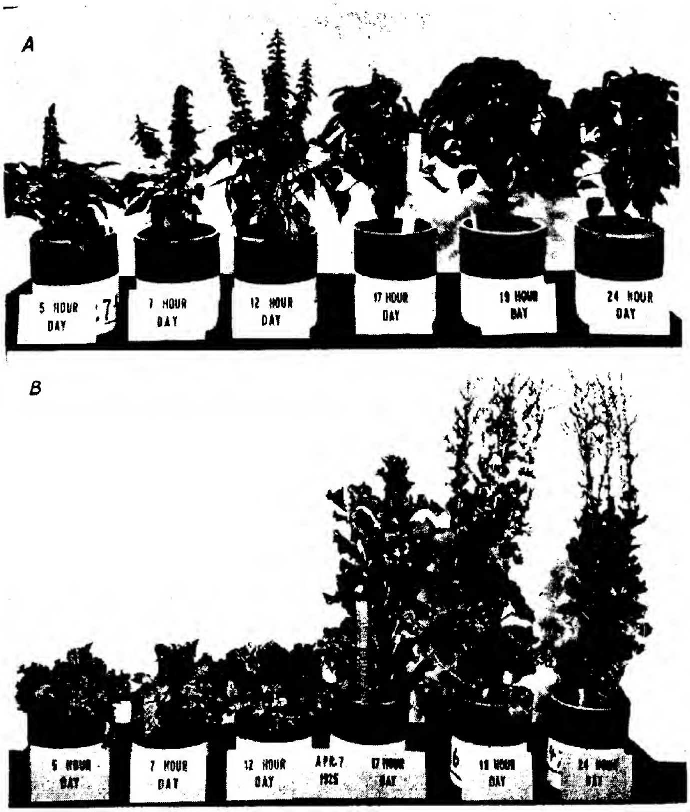


Fig. 1–9. Effect of length of day on plant growth. *A*, a short-day plant, scarlet sage; *B*, a long-day plant, lettuce. (Photograph by J. M. Arthur. Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

Temperature is another condition which affects the rate of photosynthesis. The so-called cardinal temperatures—minimum, maximum, and optimum—vary with the species of plants. In some arctic species effective photosynthesis can take place below 0°C. In the laurel cherry the lower limit is said to be $-6°$ C. and the upper limit $45°$ C. The optimum for

many common plants is from 20°C. to 22°C. From experiments with the Irish potato the following data have been reported: In full sunlight carbohydrates formed at the rate of 2.1 milligrams per 100 square centimeters of leaf area per hour at a temperature of 5°C.; at 10°C. the amount increased to 6.3 mg., at 15°C. to 8.6 mg., reaching an optimum of 13.8 mg. at 20°C.; there was then a decrease to 8.8 mg. at 25°C., to 8.0 mg. at 30°C., to 5.7 mg. at 35°C., and to 2.9 mg. at 40°C. An increase in the carbon dioxide supply raised the optimum temperature in the Irish potato about 10°C. and the maximum at least 5°C. The photosynthetic process, generally speaking, is doubled for every 10-degree rise in temperature between 0°C. and 30°C.

The rate of carbohydrate synthesis may be affected by a deficiency in soil water. If the water supply is insufficient, lessened synthesis may be due not directly to a lack of water as a raw material, but rather to unfavorable internal conditions caused by the dryness.

Restatement of Carbohydrate Synthesis

The facts are these: The carbon dioxide obtained from the atmosphere and the water obtained from the soil combine in green tissues in the presence of light to form carbohydrates, and there is a liberation of oxygen (Fig. 1–10).

The sugars formed readily pass from cell to cell. In the daytime the sugars form more rapidly than they can be transported and are often converted into starch. While we ordinarily use the starch test as a measure of carbohydrate synthesis we must agree with the statement that "the accumulation of starch in the chloroplasts is a measure, not, as has been thought, of the working capacity of a leaf, but of the excess of sugar-making over sugar transportation." Starch can be made from sugar not only by the green plastids but also by colorless plastids, and this process may take place in the dark, as in potato tubers.

The rate of photosynthesis varies in different plants and in the same plants under different conditions. Ganong has estimated that an average may be 1 gram of carbohydrate per square meter of leaf surface per hour. This he says is enough in a season to cover the leaf with a solid crystalline layer of sugar 1 millimeter (1/25 in.) thick, and it requires as much carbon dioxide as is to be found in a column of air of the same area as the leaf and 2.4 miles high. However, the carbon dioxide actually used is never taken out of such a hypothetical column. Additions to atmospheric carbon dioxide are constantly being made from the soil, especially during rains. This carbon dioxide escaping from the soil remains near the ground be-

cause it is heavy; it thus forms the chief supply for plants. It is possible that the small amount of carbon dioxide available in the atmosphere usually operates as the limiting factor in photosynthesis. The quality, intensity, and duration of light, the temperature, and the water supply are other conditions affecting the rate of carbohydrate synthesis.

A recent writer has referred to photosynthesis as the packing of radiant energy into small parcels by the choloroplasts of the chlorophyll-containing plants. The packing of these parcels of energy, which he calls "foodstuff molecules," is referred to as one of the two fundamental reactions of life; the other is their unpacking. The packing reaction is performed only by chlorophyll-containing plant cells, while the unpacking reaction "is performed by all cells, whether of the plant itself, or of the animal which eats the plant, or of the animal which eats the animal that ate the plant." It must be emphasized that the unpacking process requires oxygen, which is constantly available in nature because the supply is replenished in the packing process.

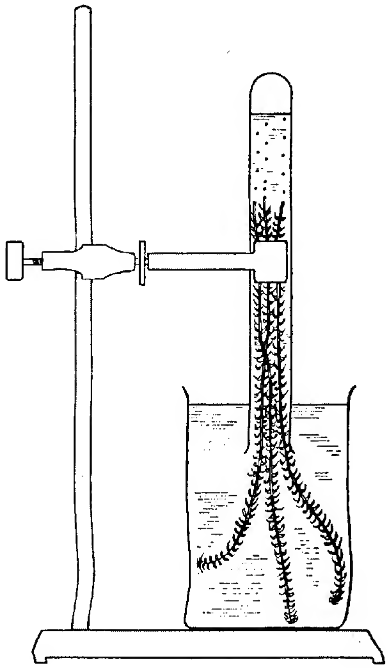


FIG. 1–10. *Apparatus for the study of release of oxygen in photosynthesis. Shoots of some plant growing under water such as Elodea may be used.*

FAT AND PROTEIN SYNTHESIS

The foods manufactured by plants are three: (1) carbohydrates; (2) fats, or fixed oils; and (3) proteins, nitrogenous in nature. We know a good deal about carbohydrate synthesis but not so much about fat and protein synthesis, yet our conception of plant nutrition would be incomplete indeed if we did not give some consideration to fats and proteins.

The fats, or fixed oils, are made up of the same elements as carbohydrates but in different proportions. The properties of fats and carbohydrates are not at all similar. The fats are relatively low in oxygen content. They are lighter than water and insoluble in it, but are soluble in ether and chloroform. We are familiar with fats and fixed oils as they are stored in such seeds as peanuts, castor beans, cotton, and corn, or as they are found in the commercial products expressed from such seeds. The fixed oils are excellent storage materials partly because of their light weight and partly because they contain a larger amount of stored energy per volume than carbohydrates. The so-called volatile oils, familiar to us for the fragrance they give to lemons, cloves, wintergreen, peppermint, etc., are different in composition and significance and are not to be regarded as foods.

Fat and Oil Synthesis

It does not seem probable that the synthesis of fats and oils is localized in any tissues, cells, or cell parts. Fats and oils are found to some extent in all protoplasm and it seems likely that it is a fundamental capacity of protoplasm to synthesize them. They are derived from carbohydrates by the protoplasm without the aid of light or chlorophyll. Specific enzymes are involved in the process. In some kinds of seeds, large quantities of carbohydrates are converted into oils while the seeds are maturing. Young almond seeds have been found to have 35 per cent carbohydrates and 2 per cent oil, as against 8 per cent carbohydrates and 46 per cent oil when old.

Protein Synthesis

In addition to carbon, hydrogen, and oxygen, proteins always contain nitrogen, usually sulphur, and sometimes phosphorus. The elements nitrogen, sulphur, and phosphorus are supplied from the soil, chiefly in the form of nitrates, sulphates, and phosphates.

The method of synthesis is uncertain and probably variable. The most important requisites are a supply of carbohydrates and available nitrogen. The green cells seem to be the chief seat of protein synthesis because the supply of raw materials is most adequate there. Carbohydrates are the basic substance out of which proteins are made. It is believed that the nitrates are first reduced to the ammonium form and that nitrogen is then incorporated with the three elements of the carbohydrates to form "building stones" known as amino acids. This is a step of great biological importance, since nitrogen is an outstanding constituent of the living protoplasm. The fact that green plants do not use free nitrogen of the air but utilize combined nitrogen from the soil accounts for the fact that nitrates are often the most

important constituent of fertilizers. Nitrogen scarcity in the soil is frequently the limiting factor in the growth and development of crop plants.

The final step in protein synthesis is the linking together of the amino acids, a step in which enzymes (substances capable of causing chemical transformations) are involved. This can be carried on in all parts of the plant, although regions where growth is most active may produce larger quantities. Proteins are so essential for the building up of the protoplasm that we may regard them as among the most important substances manufactured by plants.

Chemists recognize several different groups of proteins under such names as globulins, albumins, glutelins, etc. They will not diffuse from one cell to another until converted into amino acids by enzymes. The amino acids may be rebuilt into proteins after translocation to the growing parts or storage regions. Proteins are highly complex compounds with very large molecules. Gliadin, a protein of wheat, has the formula $C_{685}H_{1088}N_{196}O_{211}S_5$; egg albumin, $C_{696}H_{1125}N_{175}O_{220}S_8$. They exist in the cells sometimes as grains and sometimes as crystals. Their presence cannot always be made out well microscopically unless they are treated with reagents.

DIGESTION AND TRANSFER OF FOODS

Foods are synthesized in certain cells and frequently assimilated or stored in other cells. There are two reasons why foods must be moved from place to place within the plant body—one is to supply the cells which do not make food with their nutritional and respirational needs, and the other is to shift reserve materials to a place for storage. Carbohydrates are made originally only in green cells. They must be supplied to the cells lacking chloroplasts. It is evident that there must be a transfer of foods within the bodies of plants. We should know something about how this is accomplished.

Digestion

In order that foods may be assimilated, or transferred from tissue to tissue, or otherwise used, it is necessary that they be rendered soluble. These are fundamental biological processes. The reactions involved are *catabolic* in nature; i.e., they are the tearing-down processes of metabolism. The catabolic processes of making foods soluble are known as digestion.

The first foods manufactured in the leaves are the carbohydrates, sugar and starch. The higher foods are constructed from these by rearrangement

of their constituents or with additional materials. Sugar is soluble in water. Its molecules are comparatively small. Food in the form of sugar is readily transferable as such, while starches, fats, and proteins are not. We have learned that starch quickly appears in some leaves when conditions for photosynthesis prevail. But in order that starch may be made soluble it must be converted into sugar. This can be brought about by a type of chemical reaction known as *hydrolysis*. In this process there is a chemical addition of water. Such changes are effected by the activity of substances known as *enzymes*. The common enzyme in plants which changes starch into sugar is *diastase* (in reality not a single enzyme but several) and the process of conversion is called *digestion*. It is possible to demonstrate the digestion of starch in a test tube.

Diastase (of malt) can be purchased from any chemical supply company. Malt, which is sprouted grain, is a good source of diastase for the manufacturing chemist. When seeds are germinating, the enzyme is present and converts the starch into sugar. Starch paste can be prepared by putting starch into hot water. By adding a solution of diastase to a starch paste in a test tube the disappearance of starch can be proved by the iodine test. The appearance of sugar can be demonstrated by the use of a test with Fehling's solution.[1]

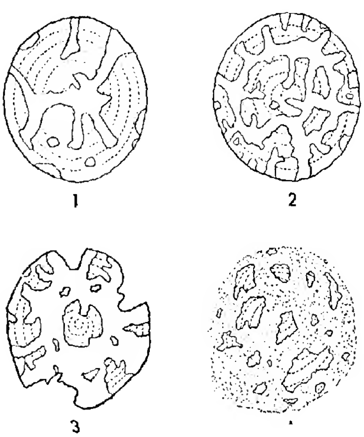


Fig. 1–11. Stages in the digestion of starch grains of barley. (After Strasburger.)

The digestion of starch grains can be observed under a microscope. They show gradual erosion. At first narrow canals appear which branch and enlarge until the grains finally become completely disintegrated (Fig. 1–11).

Starch must be digested in order to be moved out of the leaves where it first forms. It is transferred in the form of sugar. If not assimilated, starch

[1] Fehling's solution is a mixture of copper sulphate, sodium hydroxide, and sodium potassium tartrate (Rochelle salt). If glucose is present in a solution it can be detected by adding Fehling's solution and heating the mixture to the boiling point. The presence of glucose produces a yellow-red precipitate. The amount of red precipitate is a measure of the amount of glucose present.

may be reformed in some storage organ, such as stem, fleshy root, or seed. When foods are taken out of storage for new growth or for respiration, digestion must proceed once more. If reserve foods are in the form of fats or proteins they must be digested in order that they may pass from one cell to another and eventually be assimilated. The enzyme commonly associated with digestion of fats and oils is lipase. Proteins are digested by proteases and allied compounds.

Enzymes

A further word about enzymes is in order. In chemistry it is known that there are certain substances or agents called catalysts which are capable of hastening the rate of chemical reactions and yet appear unchanged at the end of the reactions. Enzymes are catalysts. They are produced only by living cells. They can, however, be isolated and separated from the living cells and are then capable of bringing about the same reactions as they do in the living tissues. Although they are produced by living cells, their activities are not dependent upon the life of the cell. They have been described as "the chemical tools of the living cells." The changes brought about by enzymes in organic substances are numerous and varied. We have shown how they are important to digestion. They are important not only to digestion but in most of the chemical changes that take place in living bodies. Not much is known of the chemical nature of enzymes. It is known that a very small quantity of enzyme can produce extensive effects. It does not seem too strong a statement to say that enzymes are fundamental to life.

The terms used to apply to specific enzymes are sometimes confusing. This comes about because there are a few old terms and a multitude of new ones, and, as a result, there is some overlapping. We referred in a foregoing paragraph to *diastase* as the enzyme concerned with starch digestion and added in parentheses "in reality not a single enzyme but several." Diastase is a collective term. In the conversion of starch into glucose there are likely several steps and several enzymes involved—amylase, dextrinase, and maltase. We used proteases in the plural to indicate that there are several. The proteases convert proteins into albuminoses and peptones. Lipase acts upon fats and oils, changing them to fatty acids and glycerin. This enzyme is able to reverse its action and bring about the synthesis of fats from fatty acids and glycerin. It is interesting that it can cause either synthesis or hydrolysis. It is believed that the water content of the tissue is a factor in determining its action. Some other enzymes may be mentioned. Sucrase reduces cane sugar (sucrose) to grape sugar (glucose) and fruit sugar (fructose). *Zymase* converts glucose and fructose into alcohol and water.

Zymase was first known in connection with yeast and was called a "ferment." *Cellulase* is an important enzyme in the fungi because it digests the cellulose walls of plant cells from which the fungi obtain their nourishment.

The Mechanism of Translocation

The movement of food in the plant body from the places of formation to the places of use and storage is known in plant physiology as *translocation.* When the insoluble foods are changed to soluble forms they are in condition for translocation. It is known that sugar in solution will move from one cell to another provided there are differences in concentration. Such a movement is called diffusion. Diffusion may account for much of the movement of sugar both in living cells and in dead conducting cells. If sugar, when moved into storage tissues, is converted into starch, the conditions for the continued entrance of the sugar into the storage cells is maintained. This is obvious when we keep in mind that in diffusion the sugar moves from the places of its higher concentration to places of its lower concentration. The conversion into a starch would lower the concentration of sugar and make possible the continued movement.

Later we will learn about special conducting tissues in plants. Everyone is familiar with the veins in leaves. These are expressions of bundles of elongated cells (called vascular bundles). These bundles are continuous throughout the roots, stems, and leaves. Some of the cells in these bundles function in the conduction of water and others in the conduction of food. The food-conducting elements are designated as phloem. They are living cells. Movements of the living matter (protoplasm) may be an aid. It seems probable that food may move in these phloem cells under pressure, which would help to account for the rapidity of its movement. It has been pointed out that in the course of a night all the food which was made the previous day may be translocated so that in the early morning the leaf may be free of food.

The phloem tissue is in the inner bark in woody plants. It is a well-known fact that removal of a ring of bark usually causes the death of trees. Death results from root starvation. All summer there is a constant movement of food downward in the inner bark for the nourishment of the parts below and for storage. If a wire or metal ring is clamped tightly about the bark, it is sometimes possible to see a swelling of the tissues just above. This results from overgrowth partially due to the stoppage of the downward movement of food. Sometimes food may be present in the wood. Thus the wood of maple trees is tapped and the sap contains sugar.

THE FOOD SUPPLY OF DEPENDENT PLANTS

Our discussion thus far has referred to the nutrition of green plants, i.e., plants with chlorophyll which synthesize their foods inside their own bodies. It is customary to call such plants *independent* plants. But there

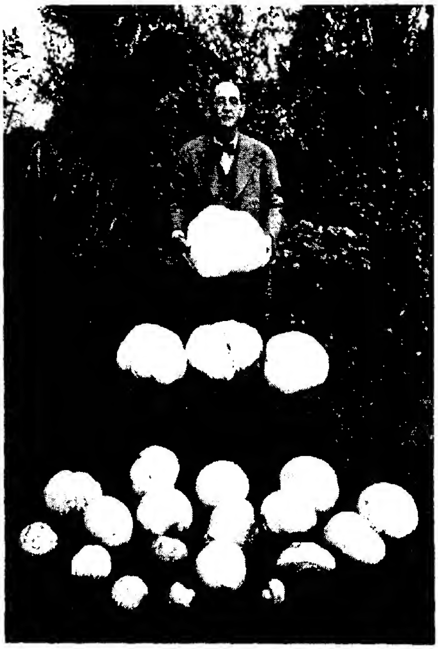


FIG. 1-12. Giant puffballs. These are chlorophyll-less saprophytes belonging to the group of plants known as fungi. (Photograph by A. B. Stout.)

are many kinds of plants which lack chlorophyll and hence cannot synthesize carbohydrates. They obtain their supply by absorbing them from some outside source. This means that they must directly or indirectly live at the expense of other organisms. On this account they are appropriately called *dependent* plants. There are two classes of dependent plants: *parasites,* which obtain their food from other living organisms, and *saprophytes,* which obtain their food from non-living organic matter or compounds. In the case of parasites we call the plant from which the food

is taken the *host*. Some parasites live within the body of their hosts. In any event they penetrate the host tissues in such a way that they can absorb food from the living cells. Saprophytes frequently live upon the dead bodies of other organisms. In fact it is due to the action of saprophytes that

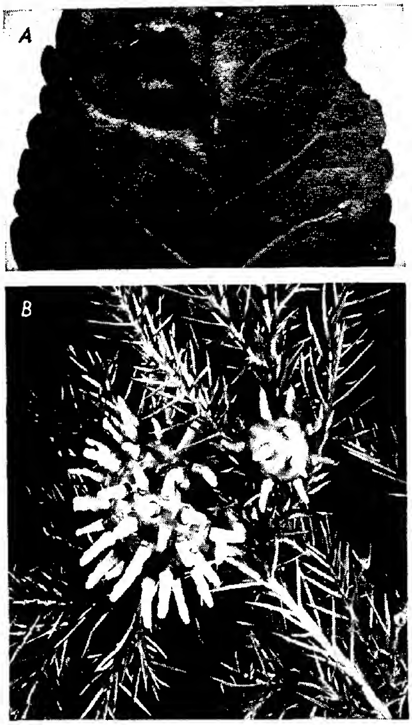


FIG. 1–13. Apple and cedar rusts. These are chlorophyll-less fungous parasites. *A*, as the rust appears on the under side of a crabapple leaf; *B*, the same fungus as it appears on galls on the red cedar.

dead organic matter undergoes decomposition and decay. As the saprophytes obtain their food they break down the complex organic substances and this constitutes decay. Our best examples of dependent plants belong to a great group known as the fungi, of which mushrooms, toadstools, and puffballs are well known (Fig. 1–12). These are saprophytes. Somewhat less widely known perhaps are such plant diseases as blights, smuts, and rusts (Fig. 1–13). Many people, however, are familiar with potato blight,

corn smut, and wheat rust. There are many more. These are caused by fungous parasites. Others are caused by bacteria. Not all of the saprophytes and parasites belong to these low classes of plant life, as evidenced by such plants as Indian pipe and dodder, which are flowering plants (Fig. 1-14). Saprophytes and parasites are able to digest, translocate, assimilate, and store food—they may synthesize fats and proteins—but they are not able to produce their own basic food from inorganic materials as are green plants.

FIG. 1-14. The Indian pipe, a chlorophyll-less saprophyte which is a flowering plant. (Photograph by L. O. Overholts.)

THE FOOD SUPPLY OF CHLOROPHYLL-LESS INDEPENDENT PLANTS

There are some kinds of bacteria which lack chlorophyll and yet are not parasites or saprophytes. Reference has already been made to the fact that they manufacture their food by a process which is a substitute for photosynthesis. These bacteria synthesize sugar from carbon dioxide and water without the energy of light. The energy necessary for this synthetic process is obtained through the oxidation of reduced iron, sulphur, manganese, or nitrogen. Since this synthetic reaction is accomplished through chemical energy instead of light energy it is called *chemosynthesis* in contrast to *photosynthesis*. Although chemosynthesis is dependent on oxidation it must not be confused with respiration. In respiration energy is released; in chemosynthesis energy is stored—it is comparable to photosynthesis, not to respiration. A few other kinds of bacteria, such as the purple bacteria, contain chlorophyll-like pigments which enable them to carry on photosynthesis.

CHAPTER 2

HOW PLANTS USE THEIR FOOD

(Assimilation, Respiration)

In the preceding chapter we described how plants obtain their food. We concluded that the materials which they take into their bodies are not food but merely the materials from which they make food. Their actual foods are the carbohydrates, fats, and proteins which they synthesize inside their own bodies. Accordingly foods for plants and animals are identical. The difference nutritionally between plants (green plants of course) and animals lies in the fact that animals cannot synthesize foods and must get their supply, directly or indirectly, from plants. It is a good thing that plants make more than they use. It is probably a safe general estimate that only three-fourths of the foods made by plants are used by them in their own growth and development, the other fourth being taken from them by animals for their nourishment.

Plant bodies contain a variety of substances. The living substance, protoplasm, the skeletal structures which support it, and many special substances are constructed directly or indirectly from foods. Foods are the source of the materials from which all the organic compounds are made. The transformation of food into protoplasm and other essential constituents of the living body is known in the biological sciences as *assimilation.*

In the preceding chapter emphasis was placed upon the fact that energy is stored in food. All living organisms, plants and animals, depend upon food as a source of energy. The process through which the stored energy of food is released and made available in the living body is called *respiration.*

With these two convenient terms it is possible to say that foods are used in assimilation as a source of building materials, and in respiration as a source of energy. Supplies of foods in excess of the immediate needs of assimilation and respiration accumulate within the plant. We frequently refer to the accumulation of food as the "storage of food." Storage food in green plants is the source of the food supply of most animals and of many

kinds of non-green plants. Assimilation, respiration, and storage must be considered if we would understand what becomes of the food which plants make.

ASSIMILATION

The actual living substance has long been called protoplasm. Huxley, the great English biologist, referred to protoplasm as "the physical basis of life." He used this as the topic for one of his famous essays. An important point that he made in this essay was that "all work implies waste, and the work of life results directly or indirectly in the waste of protoplasm." But he pointed out that happily protoplasm "has the capacity of being repaired and brought back to its full size after every exertion."

The Living Protoplasm

A part of the food supply of living things must go into the making of protoplasm, either to repair it and bring it back to full size, or to add to it, if growth is to take place. It is particularly the class of foods known as proteins which become incorporated into the protoplasm. It has been said that protoplasm is merely a complicated mixture of proteins together with mineral matter, water, and other compounds. It is, however, not generally accepted that we can regard protoplasm as a mere mixture of other substances. It must be regarded as a highly organized substance in itself.

Protoplasm is so important and so complex that its adequate consideration requires further treatment in a subsequent chapter. This brief presentation here is to bring out the point that one of the most important uses of food is to nourish the living protoplasm, even if it is true that only a small proportion of the total food synthesized by green plants actually has this function.

Skeletal Structures

In the higher animals we are familiar with the hard bony inner framework which supports the fleshy living substance, and in the lower animals with tough outer shell-like coats which protect internal living parts.

Many plants also have very real skeletons which are not only firm but tough, resistant, and in some cases extremely durable. We have only to think of the trunk of a tree together with its branches and roots to realize this (Fig. 2–1). Even leaves which may at first consideration seem soft and tender have a definite and effective system of veins. This can be realized when one sees leaves in which only the veins remain after the softer parts have disappeared (Fig. 2–2).

Fig. 2-1. Trunks of the giant redwoods, so massive that they reach heights of 350 feet, diameters of 30 feet, and so durable that they have existed for 2000 years. (Gabriel Moulin Photograph, courtesy Save-the-Redwoods League.)

Fig. 2-2. Leaf skeleton showing network of veins.

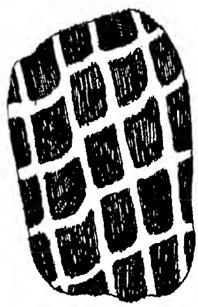


Fig. 2-3. The honeycomb (cellular) appearance of cork as copied from an illustration by Robert Hooke.

Nearly 300 years ago an English philosophical mechanic by the name of Robert Hooke discovered that bottle cork was made up of little separated compartments to which he gave the name cells (Fig. 2-3). Little did he realize the biological significance of his discovery, but it has long since been known that these spaces were originally filled with protoplasm when the cork was young and growing. Hooke used the term "cell" because he

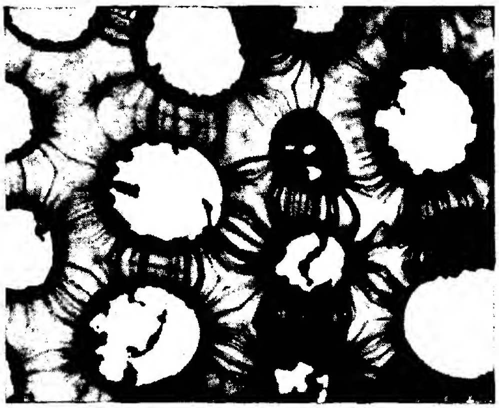


FIG. 2-4. Section of endosperm (food-storage tissue of seed) cells of persimmon, showing connecting protoplasmic threads through the greatly thickened walls. (Copyright by the General Biological Supply House, Inc., Chicago, Illinois.)

was impressed with the space, but now we think of the protoplasm together with the surrounding wall as the cell. However, we do sometimes use the term cell in the original sense as Hooke applied it. There are conducting elements and fibers in the woody tissues where the protoplasm finally dies and disappears, and yet we refer to the empty walls as cells. This cellular structure, with variations in the size and arrangements of the cells, is to be found in all plant parts as well as in the cork of the bark where first seen. The living unit of protoplasm, often called the *protoplast,* builds the wall around itself. A wall is a characteristic part of most plant cells. It is not an indispensable part of a cell. There are some plant cells and many animal cells without walls. The walls of plant cells do not completely separate the protoplasts; they are commonly penetrated by exceedingly fine channels through which pass delicate protoplasmic threads (Fig. 2-4).

The walls of these tiny units, cells, collectively form the plant skeleton. They are, therefore, a most significant structural feature of the plant body

(Fig. 2–5). Not only do they serve as a framework for mechanical support but they may serve equally well for the transportation of water and food. Elongated cells in a series form conducting strands when the walls have thin spots or perforations, especially at the ends where the cells are joined. In the woody portions of the stem the entire end walls of the cells in the series may dissolve and disappear so that real tubes are formed.

The chief constituent of the walls of plant cells is cellulose. With the cellulose other materials are usually associated. In young cells the walls are composed of cellulose and jelly-like (pectic) compounds. Chemically, cellulose is a carbohydrate made within the plant from sugar. It is estimated that more than one-third of the sugar made by a green plant is converted into cellulose. It is without doubt the most abundant plant material in the world. The chemist writes the formula for cellulose as he does for starch $(C_6H_{10}O_5)_n$, with the n representing a different value. The actual value of n is unknown for either starch or cellulose. Cellulose is not soluble in dilute acids or alkalies.

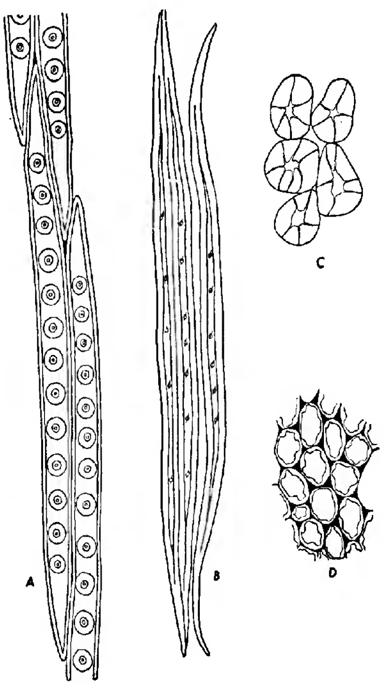


Fig. 2–5. Four important types of cells serving as mechanical elements. *A*, tracheids, from woody tissue; *B*, fibers possessing great tensile strength and flexibility; *C*, thick-walled cells known as stone cells which form supporting tissues in various parts of the plant body; *D*, collenchyma cells which provide strength and elasticity in young stems and leaves.

Cotton fibers are the nearest approach in nature to pure cellulose. Filter paper is a product consisting chiefly of cellulose. Cellulose is the raw material used in the manufacture of such articles as paper, celluloid, artificial silk, guncotton, and cellophane. The process of manufacture of these materials, and many others, comprises an interesting story.

Cellulose is definitely a structural material; but not the only one. We have

already referred to the fact that the young cells in growing parts have walls of cellulose and pectic compounds but that the composition of the walls may be altered by the addition of other substances as the cells grow to maturity. One of the substances added to cellulose walls is *lignin.* It is by the addition of lignin that wood is formed. Lignin makes the walls firmer and harder. The capacity of resisting stresses is increased in this way. The shell of a nut is also a good example of the development of hard tissue by lignification. An alteration of the opposite kind is the deposit of mucilaginous materials in the cell walls. It is well known that such seeds as those of flax and quince absorb water, swell, and become slimy because of the presence of gummy substances. Corky cell walls of bark are formed by the addition of *suberin.* The outer or epidermal cells of leaves are rendered waterproof by an external coating of *cutin.* Mineral compounds may occur in old cell walls in wood. The outer cell walls of grasses contain silica (a quartz-like compound) which gives them very great firmness. Tannins are often present in the bark of trees, from which they are extracted for tanning leather. Tannins, oils, and resins also occur in wood and are chiefly responsible for the colors of woods of commercial value.

Special Substances

Among many special substances is a group of non-nitrogenous compounds. They contain only the elements carbon, hydrogen, and oxygen. They are derived from the carbohydrates but differ from them in composition and functions. It is likely that only a small percentage of the basic sugar goes into their formation. Their functions are in some cases uncertain, but it seems that they may serve chiefly in the better adaptation of plants to their environment.

First may be mentioned the *essential* or *volatile oils.* These are not like the oils and fats which we have considered as foods. The volatile oils are aromatic or pungent. Lemon and clove oil are good examples. Other volatile oils, secreted by special glands, are responsible for the fragrance of flowers and fruits and serve to attract insects which effect pollination, or animals that aid in the dissemination of fruits and seeds.

Then there are the *organic acids* which occur in the juices of fruits and which are responsible for their tartness. Everyone is familiar with the citric acid of oranges and lemons. Malic acid occurs in apples, tartaric acid in grapes.

On the surface of some leaves and fruits there is noticeable a grayish or bluish coating. It can be observed on grapes and plums. This is due to the formation of a *wax.* Such a thick coating of wax forms on the fruits of the

bayberry that it is possible to collect and make it into candles which are highly prized as a novelty especially at Christmas time. These plant waxes are related chemically to the oils.

Under the term *resins* is included a variety of substances which are extensively employed in medicine and the arts. Like the essential oils, organic acids, and waxes, they are composed of carbon, hydrogen, and oxygen. In the plant body they accumulate chiefly in special ducts or passages. The best-known resin is a product of pine trees. Here it is called also rosin. It exudes in a semi-liquid form from the ducts in the wood when a cut or gash is made in a tree trunk. By distillation the crude exudation is separated into turpentine and the resin proper. The latter is used in soaps, ointments, and pharmaceutical plasters, and for sizing paper. Other well-known resins from evergreen trees are the balsam of the fir and the gum of the spruce. In most cases when resins are extracted from the plants which produce them they are mixed with essential oils. According to the amount of oil, which determines their behavior, they are classed as hard resins, soft resins, and gum resins. Rubber is made from the milky juice of certain temperate and tropical plants. The milky juice is called latex. This is a mixture of resins, gums, and other substances. Amber, which like coal appears to be a product of the mineral kingdom, is a fossilized vegetable resin. It is probable that amber was derived from extinct coniferous trees. Some chemists classify bitumen and asphalt as fossil resins.

It is not clear just what functions the resins serve in the physiological processes of plants. Some of them flow out of wounds in such a way as to suggest that they may serve as a protection to injuries. It does not seem likely that they ordinarily serve as food, although it is not improbable that they may do so under certain conditions.

Some of the glucose goes into the formation of a class of substances called glycosides. This term applies to certain compounds that are composed of sugars chemically combined with other substances. Some of them contain nitrogen in addition to the carbon, hydrogen, and oxygen. *Amygdalin* is probably the most familiar glycoside. It is the substance which gives the bitter taste to the seeds of almonds and plums. The peppery taste so common in the species of the mustard family (*Cruciferae*) is also due to a glycoside. *Coniferin*, found in the sap of coniferous trees, can be artificially converted into *vanillin*, which is the aromatic principle of vanilla. Some of the glycosides are poisonous. Such a one is *solanin* which is found in the potato family (*Solanaceae*). *Digitalin* is a poisonous glycoside in the leaves of the foxglove (*Digitalis*) which has a use in medicine.

There is uncertainty regarding the value to plants of a class of substances

known as *alkaloids*. Since many of them are bitter in taste and poisonous in nature they may protect the plants against destructive animals. Chemically, the alkaloids contain nitrogen and are related to, and doubtless formed from, the proteins. Among the more important alkaloids may be mentioned strychnine, from *Strychnos* beans; nicotine, from tobacco leaves; morphine, from poppies; caffeine, from coffee berries and tea leaves; cocaine, from coca leaves; muscarine, from a mushroom (*Amanita muscaria,* Fig. 2–6); and quinine, from the bark of the cinchona tree (Fig. 2–7). Some of these have large economic or medicinal uses.

FIG. 2–6. *Amanita muscaria,* the mushroom which produces the poisonous alkaloid, muscarine. (Photograph by L. O. Overholts.)

Some of the plant food is used in the formation of pigments. The chlorophylls and carotenoids were discussed in Chapter 1, and reference was made to the anthocyanins. The latter pigments are the basis of the red colors of autumn foliage, of the red color of beets, and of the red and blue colors of flowers and fruits. The red color of some flowers is associated with an acid reaction, and blue with an alkaline reaction. This can be demonstrated by placing petunia flowers in ammonia or acetic acid. Other plant pigments which man has used as dyestuffs are haematoxylin, henna, indigo, litmus, and madder.

Other important substances synthesized within the tissues of plants are *enzymes, vitamins,* and *hormones.* Enzymes are necessary in digestion, as previously explained, and in practically all chemical transformations (metabolism) taking place in the living organism. Vitamins, known to be essential to animal life, are probably as essential to plant life. Hormones are substances which influence growth. All of these substances, although common in plants, are present in such small quantities that no substantial part of the materials within the plant body is required for their formation.

RESPIRATION

We have already indicated that when we are reviewing the various uses which plants make of their food, we must give a prominent place to a consideration of the way they get their energy from it, for this is one of the

important uses of food. It is a well-recognized fact that animals develop and expend energy. We associate activity with energy. Because plants do not move about and seem never to be active or to exercise force it is not a

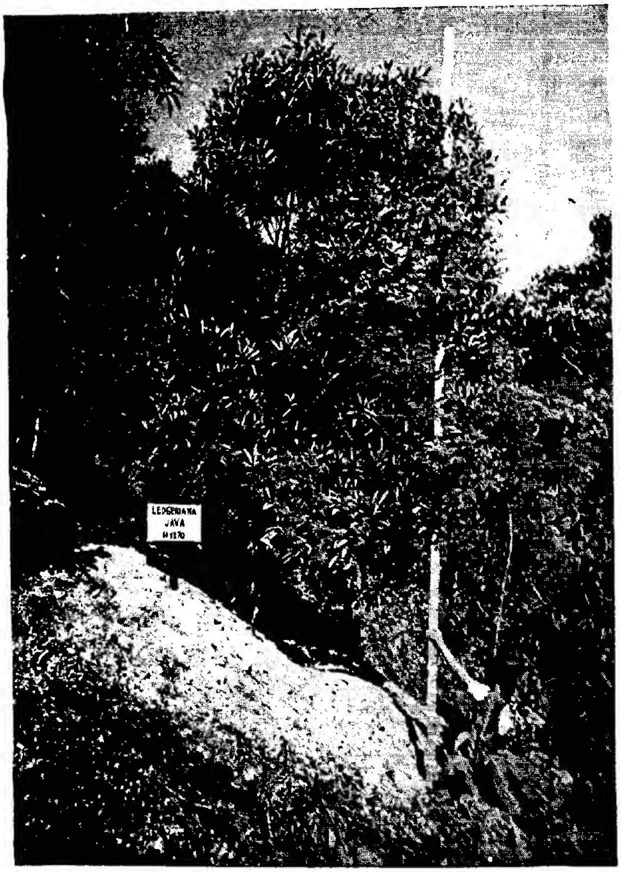


Fig. 2–7. Cinchona; the bark is the source of quinine. (Photograph by J. R. Shuman.)

generally recognized fact that they develop and expend energy. The Biblical saying, "Consider the lilies of the field, they toil not neither do they spin," is an expression of the concept that plants are passive beings.

Although plants do not move from place to place it can be proved that their parts move in a really energetic manner. It is because their motions

are so slow that we fail to appreciate them. Fortunately it is possible to magnify these actions so that we may get an entirely different impression. This can be done by taking what are known as time-lapse pictures on a film and then running the film in a moving-picture projector. We then see stem tips moving upward, nodding, and turning energetically about; roots penetrating the soil with curious twisting motions; flower buds opening and closing with jerky and often sudden movements; tendrils sweeping through the air until, striking a support, they grip it and pull the plant toward the support. Even without the aid of the movie camera we have all seen seedlings which have broken through the soil in a way to leave no doubt of a power within them.

And so we need have no hesitation in concluding that plants, as well as animals, carry on activities which require the expenditure of energy. This energy is made available through biological oxidation, the process called *respiration.* Ordinarily oxygen is taken into the living cells, with the result that substances, usually organic compounds, are broken down. The splitting of a carbon compound such as sugar releases energy; the energy was in the food molecules. A considerable portion of the food manufactured by plants is used as a source of energy. The original source of the energy is the sunlight which was locked up when the carbohydrates were manufactured in the process of photosynthesis. The *kinetic* (active) energy of light is stored in the food as *potential* (resting) energy. To be utilized, this potential energy must be reconverted into kinetic energy. All living cells are able to bring about biological oxidation "in such a way that energy is not liberated as heat but in some other more useful form." Combustion is a homologous oxidation process by which energy is similarly converted in non-living bodies. Combustion results in the release of energy principally as heat, but with the proper machinery this form of energy can be transferred into motion and made to do work. In living organisms protoplasm is the medium which transforms into motion and work the energy released by respiration.

Proof of Gaseous Interchange

The fact that animals must breathe in order to exist is so well recognized that no one asks for proof of it. But it required experimental investigation to prove that plants take in oxygen and give off carbon dioxide. A hundred and more years ago this question had been investigated and correctly interpreted. And yet some prominent workers long afterward expressed disbelief. The opposition held that it had been proved positively that plants take in carbon dioxide and give off oxygen (which they do in photosynthe-

sis) and that it was absurd to suppose that both processes could be carried on at the same time when one was the reverse of the other. But this is just what occurs. Of course both processes do not take place in all tissues and at all times simultaneously, but under certain conditions they do proceed together in the same cells. Green tissues alone take in carbon dioxide and give off oxygen, and then only in the light, whereas both green and non-green tissues in both light and darkness take in oxygen and give off carbon dioxide.

That oxygen is absorbed can be proved, but its demonstration is somewhat difficult. If seeds are germinated and grown for several days in a

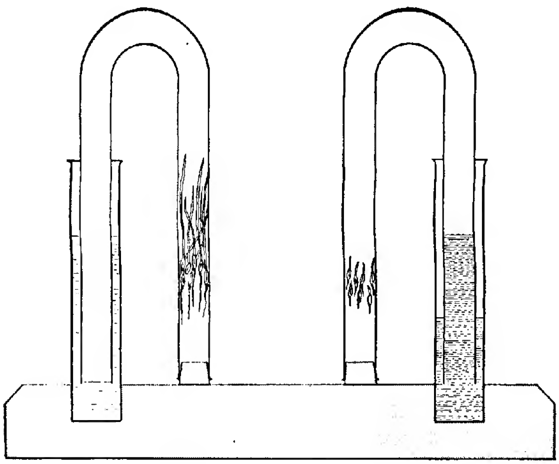


FIG. 2–8. Diagram of apparatus to show the necessity of oxygen for the respiration of germinating seeds. See text for explanation.

closed chamber, a chemical analysis reveals that oxygen has disappeared. If germinating seeds are placed in a closed chamber from which all the oxygen has been removed they cease growing immediately, whereas in a chamber with all conditions the same, except that the normal amount of oxygen in the air is available, they keep on growing normally for some time. In the first case the lack of growth indicates lack of energy, which is explained by the failure of respiration due to the absence of oxygen. To set up such an experiment two U-tubes can be used to advantage (Fig. 2–8). The germinating seeds (oats are especially good) are placed in some moist cotton near one end and that end stoppered. Some pyrogallic acid is pressed into the open end of the tube from which the oxygen is to be removed. If

care is taken, the acid will adhere to the glass and stay in place. This end can then be carefully lowered into a vessel containing potassium hydroxide. Pyrogallate of potash is formed and the oxygen is absorbed. Air pressure forces the pyrogallate up the tube so that it comes to occupy one-fifth of the space if all the oxygen is removed. The end of the other tube is placed in a vessel of water so that all conditions are exactly duplicated except that the ordinary oxygen of the air is present.

That living plants, or plant parts, give off carbon dioxide can be demonstrated by a simple method. The plant parts are placed in a wide-mouthed

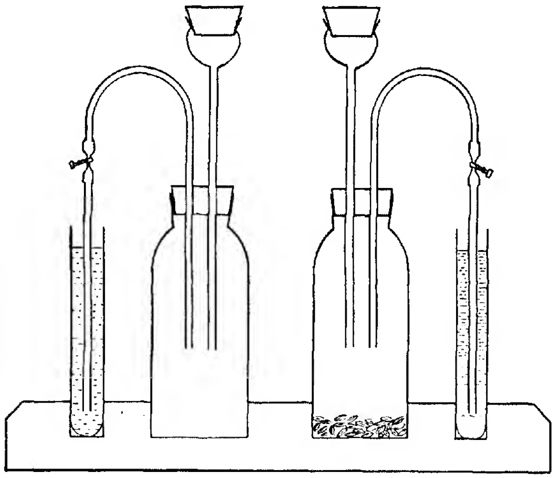


FIG. 2-9. Diagram of apparatus to show that carbon dioxide is given off in respiration. See text for explanation.

bottle (Fig. 2-9). Through the stopper is inserted a thistle tube and a U-tube which leads into a test tube containing limewater. A stopper should be placed in the thistle tube and the U-tube should have a short section of rubber tubing furnished with a clamp. In this way the bottle is airtight and can be left overnight or at least for several hours. If carbon dioxide is evolved, it is possible to detect it by its property of turning limewater milky. The gas in the bottle can be forced to bubble up through the limewater in the test tube by pouring water into the bottle through the thistle tube. If the limewater turns milky, carbon dioxide is present. By using a similar setup without the plant parts as a check it can readily be demonstrated that the carbon dioxide present in an equal quantity of air from an

empty bottle will not turn limewater milky. Any living plant parts will suffice for the experiment, but the best results are obtained when parts that are actively working are used; germinating seeds, opening flower buds, or growing mushrooms are good materials. If green parts are used it is well to keep the apparatus in the dark so as to avoid complications from photosynthetic activity.

Respiratory Mechanisms and Conditions

In ordinary respiration, which involves interchange of gases between protoplasm and the atmosphere, it is clear that the process can proceed in a simple manner with unicellular organisms, or with relatively simple multicellular organisms, whether they be animals or plants. But in larger multicellular bodies comparatively few cells are in direct contact with the air on the outside of the body and those that are so situated may be more or less impermeable. It follows that provisions for gases to pass back and forth between the atmosphere and the individual internal cells are very necessary. Most people are familiar with various mechanisms in animals such as gills, tracheae, and lungs. In the higher animals we can divide exchange of gases into two steps: (1) the interchange of gases in the lungs, and (2) a similar interchange between the body cells and the surrounding fluids. We also know that the higher animals do not wait for air to enter the lungs by its own circulatory movements but that the air is taken into the lungs and expelled rhythmically in the process commonly known as breathing.

There are no respiratory movements of plant parts. In the higher plants gases enter through openings in the epidermis (*stomata*) and through small areas of loosely arranged cells in the bark (*lenticels*). On the inside they pass through intercellular spaces. All gases diffuse from places of abundance to places of scarcity, and this purely physical process, known as diffusion, brings about the entrance and exit of gases to and from the plant body.

There are a number of conditions that affect the rate of respiration. Some of these conditions are internal factors and some are of an external nature. The age of the plant, its activity, the acidity of the cell sap, and the amount and concentration of respiratory materials may be mentioned among the internal factors. In dormant structures, such as seeds, buds, and bulbs, respiration proceeds feebly; but when growth is renewed it proceeds rapidly. Wherever tissues are growing actively the rate of respiration increases. If there is not an adequate supply of food, the rate falls.

Temperature has a direct effect on the rate of respiration. There is some respiration as long as there is life. At extremely low temperatures the rate is exceedingly low. As the temperature rises, the rate of respiration approxi-

mately doubles for each 10°C. rise until a maximum is reached. Light has an indirect effect on respiration; it is not necessary for respiration. We know that respiration proceeds at night, but in green tissues the rate is more rapid in the light. This may be due to the increased supply of carbohydrates as respiratory materials. The supply of oxygen is rarely a limiting factor in respiration since normally a great deal more is present in the atmosphere than is used. Some plants and plant parts continue to live and give off carbon dioxide in the absence of free oxygen. They carry on what is known as *anaerobic respiration*. This topic will be discussed later. The amount of water present has a direct effect on respiration. We have referred to the low rate of respiration in dry seeds. Increasing the water content increases the rate until a maximum is reached. Some chemical compounds, such as chloroform, ether, acetone, and formaldehyde, are toxic to plant tissue because of their effects on respiration. Strong doses may check respiration and cause death, but weak doses may act as stimulants increasing the rate of respiration, at least for a time. Diseases and injuries may act as stimulants to the respiratory process. Injuries under certain conditions are followed by increased growth resulting in the healing of the wound. The energy for the new growth is supplied by increased respiration.

The Chemical and Physical Aspects of Respiration

We have referred to respiration as a process inside of living cells in which oxygen unites with organic matter and breaks it down into simpler products. The chief products of this breaking-down process are carbon dioxide and water. The process goes on under the influence of respiratory enzymes called oxidases and is highly complicated. Carbohydrates disappear and carbon dioxide and water appear. Centering our attention on these end substances, we can express the reaction by a chemical equation, thus:

$$\underset{\text{Glucose}}{C_6H_{12}O_6} + \underset{\text{Oxygen}}{6\ O_2} = \underset{\substack{\text{Carbon}\\\text{dioxide}}}{6\ CO_2} + \underset{\text{Water}}{6\ H_2O} + \text{Energy}$$

This equation represents the complete respiration of glucose. As it stands, the volume of oxygen taken in is equal to the volume of carbon dioxide given off. For various reasons this is not always the case. But even if the process is not as simple as the equation would seem to indicate, the equation is correct for the two extremes of the process. Attention is drawn to the fact that this equation is the exact reciprocal of the one given in Chapter 1 as the photosynthetic equation.

Living organisms, both plants and animals, utilize atmospheric oxygen

in respiration. The constant respiration of organisms would eventually exhaust the available supply of oxygen in the atmosphere, were there not some means for releasing oxygen and making it again available for respiration. Such a means exists; it is part of the process of photosynthesis. Car-

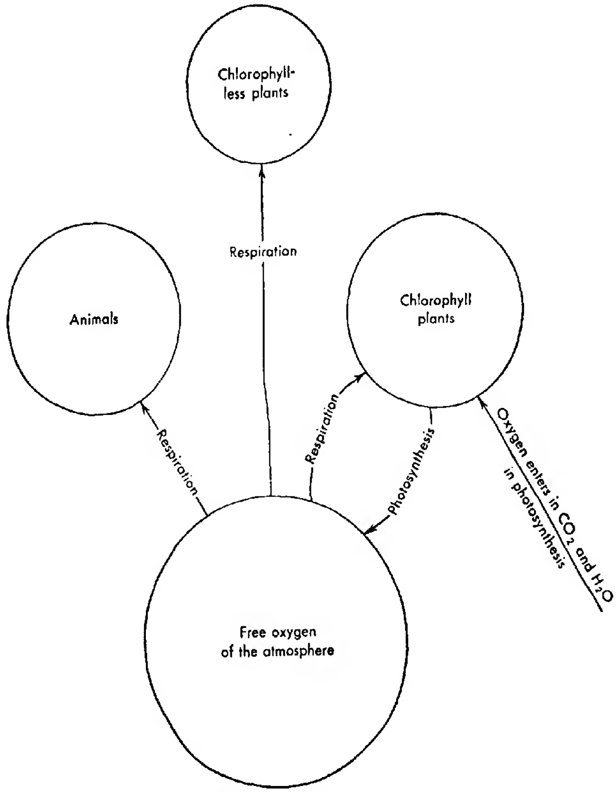


Fig. 2–10. Circulation of oxygen.

bon dioxide and water are formed in respiration; they are combined in photosynthesis to produce sugar with the liberation of oxygen. Through photosynthesis the supply of oxygen in the atmosphere is replenished. This is another way in which plant life is indispensable to all life. These facts are summarized diagrammatically in Fig. 2–10.

The respiratory equation indicates the release of energy. We have al-

ready emphasized that energy is the fundamentally important feature of respiration, and this fact must not be forgotten. Since the chemically similar process of combustion produces heat, the question naturally may arise whether or not this is true of respiration. The answer is that some of the energy released by respiration is in the form of heat. If soaked living seeds are placed in a thermos bottle provided with a thermometer through the stopper, the evolution of heat can be observed. If soaked seeds which have been killed by hot water are used for comparison, they will be found not to produce heat.

If the statement is correct that the source of the carbon released in the carbon dioxide is the solid material inside the plant, then it follows that respiration always results in a loss of weight. This is true and can be proved readily. Of course the growing plant gains in weight. This is the case because its addition of new materials by photosynthesis more than offsets its losses from respiration. To try an experiment, divide some seeds into two lots of equal weight and arrange them for growth in water cultures. Keep one lot in the dark and the other in the light. After a time those which have been in the dark will be long and spindly and will look larger than those which have grown in the light. But if the water is dried out of them and the dry weights are compared, it will be found that those grown in the light are much heavier than those grown in the dark. Those in the light have made added food, whereas the others have been losing without any additions and they weigh not only less than the seedlings grown in the light but actually less than the seeds from which they grew.

Anaerobic Respiration and Fermentation

We have already referred to the fact that plants which ordinarily require free oxygen for respiration may, when placed in an atmosphere devoid of oxygen, continue to live for a while and to liberate carbon dioxide. Physiologists call this *anaerobic respiration*. No oxygen is consumed. Energy is liberated but to a less extent than in respiration where oxygen is consumed, because the compounds yielded still contain much of the energy in the original compounds. In other words, the process does not result in complete oxidation. Carbon dioxide is formed. A common form of anaerobic respiration, or fermentation, is represented by the following equation:

$$\underset{\text{Glucose}}{C_6H_{12}O_6} = \underset{\substack{\text{Carbon}\\ \text{dioxide}}}{2\ CO_2} + \underset{\text{Alcohol}}{2\ C_2H_5OH} + \text{Energy}$$

The yeast plant regularly produces this effect in a sugar solution. This process is ordinarily called *fermentation* but it is actually the respiration of the yeast plant. There is a release of energy which is utilized by the yeast cells for their growth, carbon dioxide is liberated into the liquid, and alcohol is formed. When we use yeast in bread-making, our objective is the release of carbon dioxide which raises the bread. When we use yeast in the fermentation of grape juice our objective is the alcohol which is the secondary product. In neither case are we interested in the yeast plant itself except for the effects which it produces as it carries on its respiration.

Without doubt, alcoholic fermentation is the kind most familiar to us, *but there are other sorts. Bacteria cause milk to sour and butter to become* rancid. Carbon dioxide is produced in both, but the secondary products are lactic acid and butyric acid respectively. Fermentation is a less efficient method of obtaining energy than is ordinary aerobic respiration and yet it *is the sole method used by many bacteria and fungi.*

Decay of dead organic substances is in reality a form of fermentation brought about by bacteria and fungi. These organisms in their respiration break down complex substances into simpler ones until carbon dioxide and water are finally formed. Other products formed include other elemental substances and gases which are responsible for the odors that sometimes accompany the decay of organic matter. Bacteria which cause certain diseases produce their effects through poisons known as ptomaines. These bacteria act on the blood or body tissues in a manner similar to the way that yeast acts on sugar. They are carrying on respiration and obtaining energy. The ptomaines are products that are left over in these intramolecular rearrangements as alcohol is left over when yeast acts on sugar. It is a well-known fact that fermentation, decay, and certain phases of disease are caused by yeasts, fungi, and bacteria. In these processes simple organisms destroy organic matter and reduce it to carbon dioxide, water, and other elements from which it was originally formed. It is perhaps not so well known that these processes cannot be effected in any other way than through the activity of these organisms. It is surely not so well known that these processes are the results of the respiration of these organisms whereby they obtain their energy. In these organisms intramolecular respiration, which does not require free oxygen, is a complete substitute for ordinary respiration, which requires free oxygen.

STORAGE OF FOODS

In our discussion of the uses of food, we saw how food goes into the production of protoplasm, skeletal structures, and special structures, and how it is oxidized to release energy. But in many plants not all of the food made is used at once and directly in these ways. In fact most plants have both the capacity and the habit of making more food than required for their daily needs. As the surplus accumulates, it is stored. Some plants have special reservoirs or storage organs such as tubers, bulbs, fleshy roots, etc. Of course *it must be clear that storage is not in itself a use of food but a method* by which food is reserved in a place and in a form in which it is available for a future use. A large part of the foods which animals take from plants is in the form of stored or reserve food.

Since many plants exist in regions where conditions for food manufacture are favorable only part of the time, stored food must be utilized for respiration during the unfavorable season and must supply materials for the early growth in the next favorable season until new manufacturing parts are produced and brought into activity.

The amount of food stored, and the place and conditions of storage, are dependent upon the kind of plant. In trees great quantities of food are stored in the twigs, branches, trunk, and roots. In the spring there is a rapid movement into the unfolding buds. Many plants which do not have woody parts above ground but whose underground parts live over from year to year (perennials) have food stored in the roots or in specialized underground stems (Fig. 2–11). The thick root of the dandelion is a good example of root storage. The sweet potato is another. In the Canada thistle and the wild morning-glory underground stems are the storage parts. In lilies and hyacinths we speak of the structures as bulbs. Here the storage occurs in thickened leaf scales. The corm of the gladiolus is a thickened stem. In the common potato and the Jerusalem artichoke stems are the storage organs, for the tubers are but thickened and modified stems. In plants which live for only one growing season (annuals) food is stored in the seeds where it is available for the nourishment of the young seedling until the new green parts are producing a new food supply. In plants which live for two seasons, producing seed at the end of the second season (biennials), food is stored both in the overwintered roots and in the seeds.

All classes of foods (carbohydrates, fats and oils, and proteins) are found in storage organs. Starch is a common form of storage food. If we cut thin sections of a common potato and examine them under the microscope we find the cells packed with starch grains. If similar sections of the cotyledon

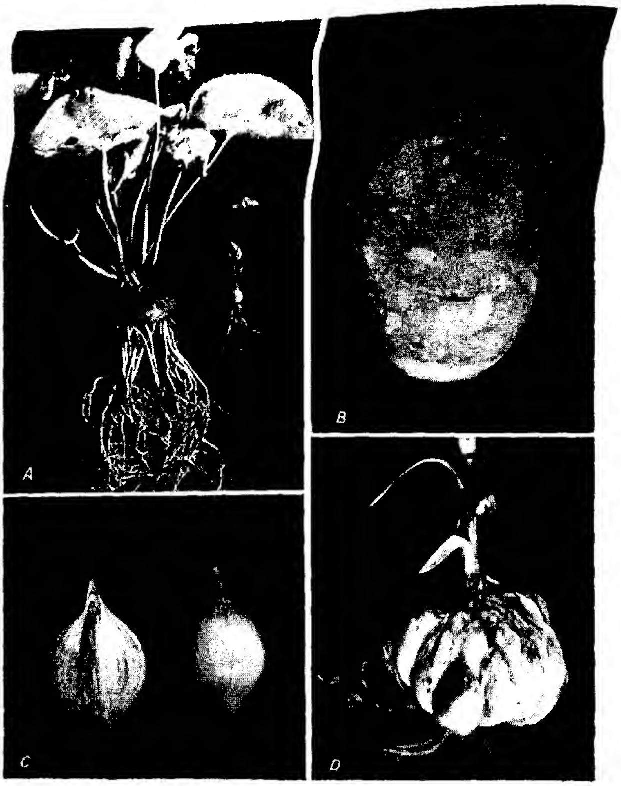


FIG. 2-11. Food storage organs. *A*, corm of cyclamen; *B*, tuber of potato; *C*, onions; *D*, lily bulb.

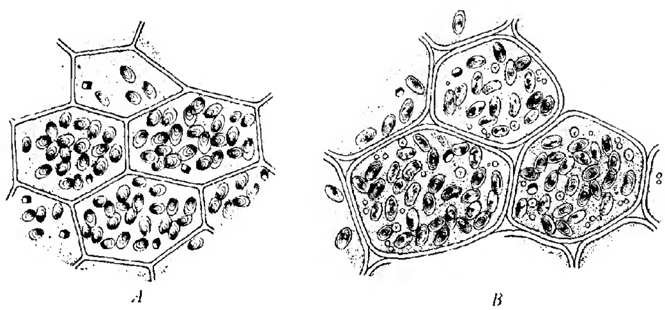


FIG. 2-12. Food storage cells. *A*, sections of cells of potato packed with starch grains; *B*, cells from the cotyledon of bean with starch grains, fat droplets, and protein granules. (Drawings by Vega Ihsen.)

leaves of the embryo in the seed) of a bean are examined we find not only starch grains but also fat droplets and protein granules. Sugars are stored in many fruits, fats and oils in certain seeds, proteins in the grains. In some cases *the walls of the cells become greatly thickened and serve as reserve food (Fig. 2-12). Here the composition is sufficiently different chemically* from cellulose to be designated by the term hemicelluloses. They are found in such seeds as dates and coffee and in the nut of the ivory palm. They cause these structures to be very tough and hard.

CHAPTER 3

THE ORGANIZATION OF PLANT BODIES

(Protoplasm, Cells, Vegetative Organs)

It must be evident to the most casual observer that different kinds of plants vary greatly in form and size. Trees are large, usually with a strong trunk and branching crown; shrubs are smaller and branched but usually without any central trunk; and there are the countless smaller non-woody plants commonly called herbs. In addition there are mosses and liverworts and seaweeds which are recognized as plant life. We cannot escape the conclusion that the forms of these many kinds of plants are variable and diverse. At this point we are not concerned with an attempt to discover the causes of the variations in forms; but we should consider how great the variety of form really is, and how much the different kinds of plants have in common, although appearing so unlike.

It will be recalled that life is always associated with a substance long since known to students of biology as *protoplasm*. In the body of all living things, plant or animal, the real active living matter is the protoplasm. "The bodies of animals and plants are composed of protoplasm and its products." We come, therefore, to the realization that regardless of the form, size, or color of the body, all living things possess in common this basic material, protoplasm. Wherever there is life, there is protoplasm; "an organism is, in fact, an organized mass of protoplasm interacting with its environment." This does not explain what life is; it merely asserts that life is always associated with a certain kind of matter.

THE CELL

While it is true that life is universally associated with protoplasm we must guard against the conception that the bodies of living things always consist only of this substance. We also must avoid thinking of protoplasm as a solid or homogeneous mass. In its simplest condition it may be visualized as a thick, viscid substance something like the white of an egg. Within

the protoplasm may be included foreign particles, crystals, and droplets which are not part of the protoplasm but are completely surrounded by it.

If we examine under a microscope a drop of water containing some of the slime which collects at the bottom of fresh-water pools and similar locations, we may find a tiny moving animal form known as the amoeba.

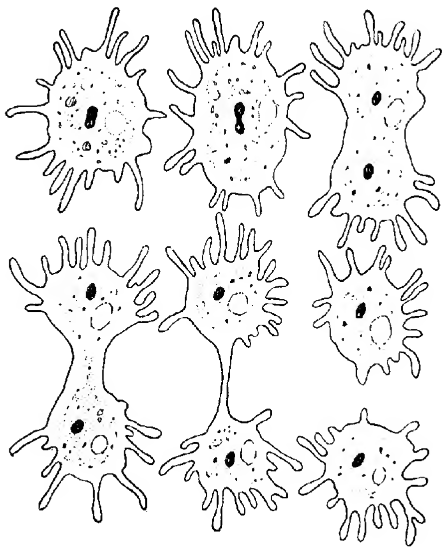


FIG. 3–1. An amoeba in several successive phases of division. (Redrawn from Woodruff.)

It is in reality nothing more than a little irregular particle of protoplasm. This simple organism is constantly changing its shape and its position. It does this by a kind of streaming motion. A projection forms on one side and much of the substance seems to stream into it. Then another similar projection appears and the streaming is continued. It is evident that the body is soft and semi-fluid, yet it does not mix with the water and always retains a well-defined outline despite the irregular shape. If we look carefully we can distinguish a denser globule within, which preserves its form no matter how much the shape of the protoplasmic mass changes; this is termed the *nucleus*. Foreign particles—usually minute fragments of an organic nature —are taken into the interior of the protoplasm. The amoeba increases in size. Soon a remarkable change may take place. A fissure may appear that keeps on developing until the amoeba is divided into two parts which

finally become completely separated so that two distinct amoebae result from the division of the one. The nucleus also divides, so that there are now two organisms in all respects like the original one (Fig. 3-1).

In their earliest stages the bodies of animals and plants, regardless of their larger size or later form, consist of a single minute particle of protoplasm more or less similar to an amoeba, except that it is rounded rather than irregular in shape. Soon this original particle divides into a number of parts which, instead of separating, as in the case of the amoeba, remain associated together to form a cluster or clump of minute particles of protoplasm. Each of these protoplasmic units is called a *cell.* A single cell constitutes the entire body in the smallest and simplest forms; a vast multitude of cells appears in the organization of the large and complex forms.

In the multicellular bodies, typical plant cells are separated by some intercellular substance and in addition each cell is surrounded by a relatively firm wall. The cells are thus rather distinctly separated from one another. The cell wall is a product made by the protoplasm. In contrast to plant cells, most animal cells are without walls, but they, too, are separated by intercellular substances. We have previously discussed cell walls and have pointed out how they form the skeleton of the plant. The earlier workers were much impressed with the discovery of the cellular structure of plant bodies. The cell walls were conspicuous as these workers carried on studies with the microscope. Not until the middle of the past century was it realized that the protoplasmic contents, and not the walls, were the real units of activity. While it is necessary to give attention to the structural features of cells, we can form proper concepts only by considering also the relation of the cells to the life process of the organism of which they are parts.

If we examine a thin longitudinal section of the tip of a root of a higher plant (a hyacinth root tip is especially good) with a magnification of about 450 diameters we find that it consists of nearly rectangular cells filled with protoplasm, and separated by delicate walls (Fig. 3-2). If the section has been stained and prepared according to the usual technique there will be clearly distinguishable in each cell a darker round body of comparatively large size. This body is the *nucleus.* Filling in the space between the nucleus and the wall is a lighter substance appearing more or less granular or reticulate; this is called the *cytoplasm.* The life of the cell depends on the interaction between these two components.

The observation of sections farther back from the growing tip, or in other parts of the plants where the cells are older, reveals that they are no longer filled with protoplasm. As the cells have enlarged there has not been a proportional increase in the amount of protoplasm and there are clear

spaces in the cytoplasm which look as if they were empty. These clear spaces are cavities called *vacuoles.* In life, the vacuoles are filled with a watery fluid, the *cell sap.* As the cells continue to enlarge, their whole central portion may be occupied by a single large vacuole. The cytoplasm then

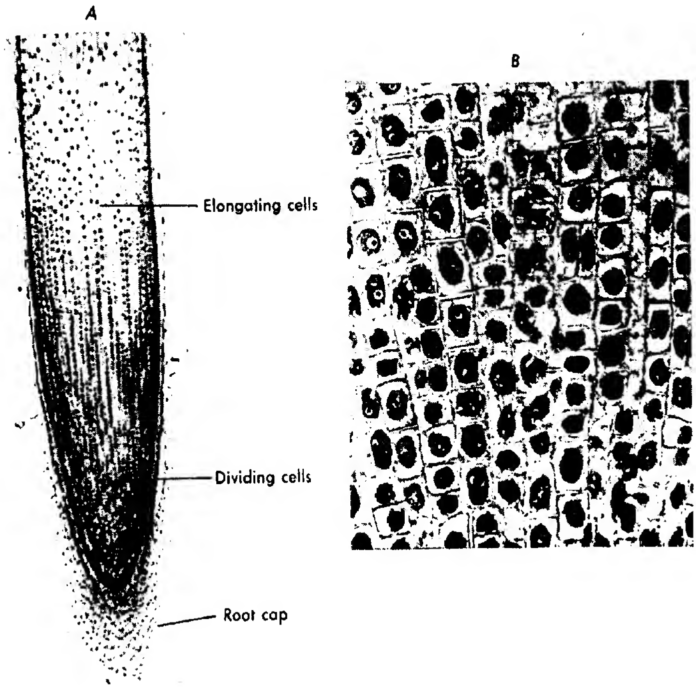


Fig. 3–2. Lengthwise sections of root tips. *A*, lower magnification; *B*, higher magnification showing the rectangular cells, walls, cytoplasm, and nuclei. (*A* reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

forms only a comparatively thin layer lining the cell wall and surrounding the nucleus. The nucleus is enclosed within the cytoplasm.

If a section through a living green leaf is examined we find in the internal cells a number of green rounded bodies, *plastids,* also suspended in the cytoplasm. These plastids contain the pigment chlorophyll and are known as *chloroplasts* (Fig. 3–3); they have already been described as the seat of photosynthetic activity. Other cells contain plastids which are de-

void of pigments. Such plastids are known as *leucoplasts.* Still other cells such as those in the petals of flowers and in the skin of fruits have plastids containing red, yellow, and other colored pigments. These are known as *chromoplasts.*

In botanical science it is customary to designate the living constituents of a single cell (nucleus, cytoplasm, and plastids) as the *protoplast.* A plant protoplast is to all intents and purposes comparable to the entire animal cell.

FIG. 3-3. Section through a leaf showing cells with chloroplasts.

The Protoplasm

If we remove some of the hairs which are so noticeable in the flowers of the garden spiderwort (the wandering Jew, a tropical plant common in greenhouses, is equally good), or some of the hairs from the young leaves of squash, and place them in a drop of water on a glass slide under a thin cover glass, we have a microscopic preparation (Fig. 3-4). Under the microscope we can study the living protoplasm. There are large vacuoles in the cytoplasm, but we find it lining the walls and surrounding the nucleus, and also as gray granular strands or threads. By carefully observing the cytoplasm, we may detect a streaming motion within it. Actually here within the bounds of the cell are movements comparable to those described in the amoeba. Sometimes there is a current in the layer along the wall. In other cells motion may be more noticeable in the strands. These strands or threads may alter their form, and as the movement continues, the position of visible granules changes; they are evidently transported by the flow-

FIG. 3-4. Cell from stamen hair of the wandering Jew. When living cells are observed under the microscope a streaming motion can be seen along the cytoplasmic strands.

ing protoplasm. A similar preparation of a thin leaf of ditchmoss (*Elodea*) would show the chloroplasts in circulation. This streaming of the protoplasm within the cells is fascinating to observe. To most of us it seems a visible proof of its living condition. In many living cells there are no such streaming movements, or if any are present they are so slow as to be imperceptible. In any event we must realize that perceptible movements are not typical of all living cells.

Under the microscope the living protoplasm is usually inconspicuous, translucent, colorless or grayish, and appears more or less granular. The protoplasm of plastids may appear to be colored because of the presence of pigments. Ganong says, "A white-granular, slow-moving jelly; that is what protoplasm looks like, and that is precisely what it is . . . and try as one will, he can see little more."[1]

Physically, protoplasm consists of various interacting substances and compounds, both inorganic and organic, dissolved and suspended in water, which makes up 70 to 90 per cent of its weight. In the solid matter the protein content about equals in quantity the combined content of sugars, salts, and fats.

According to a foremost investigator, the laws of physics and chemistry dealing with pure liquids and true solutions are applicable only in a general way to protoplasm. In the words of this investigator, "Protoplasm is an intimate association of three distinct types of systems, a true solution, an emulsion, and a jelly. The salts and sugars in protoplasm are in true solution. The fats form an emulsion. The proteins exist as a jelly, which may be either very firm or fluid enough to flow freely."[2] One of the characteristics of protoplasm is the possibility of its undergoing changes in viscosity, that is, its capacity to change from a less viscous to a more viscous condition, and the reverse. The viscosity varies in the different parts of a cell and in the cell as a whole at different stages of development.

The chemical structure of protoplasm remains uncertain despite all the analytical studies. This is due to the fact that the necessary chemical laboratory procedures turn protoplasm into a substance quite unlike what it was when alive. We have said in an earlier paragraph that we must think of protoplasm not as a mere mixture of other substances, but as a highly organized substance in itself. However, it has been described as "a state of physical and chemical activity in a mixture of many different chemical compounds." Another writer lists thirty compounds that have been found

[1] W. F. Ganong, *The Living Plant*, Henry Holt & Company, Inc. Copyright 1913 by Henry Holt & Company.

[2] Reprinted by permission from *Physiology of Plants* by W. Seifriz, published by John Wiley & Sons, Inc. Copyright 1938 by William Seifriz.

in the protoplasm of one of the lower plants and ends with *undetermined matters, etc.* This will serve to emphasize its complexity. None of the substances or compounds listed are alive. Some workers believe that there is actually a living constituent which has not been identified. One says that "the essence of protoplasm is in the activity rather than the mixture." Ganong's account, although written several years ago, is still reasonable. He says, "Protoplasm, therefore, is probably composed chemically of two classes of materials; first, a very small amount of a distinctly living constituent, not yet identified, but consisting in the fibres, or the continuous substance of its physical texture; and second, a very large amount of various non-living substances, nutritive and other, which are under the control of the living constituent."[3]

While a majority of the known chemical elements have been found in protoplasm, only twelve are common: carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, potassium, sodium, calcium, magnesium, iron, and chlorine. Of these, the first four make up the principal part by weight. The most common of all compounds in protoplasm is water. It is a solvent for inorganic salts and for organic compounds. The gases present are oxygen and carbon dioxide. Protoplasm generally gives a neutral or an alkaline reaction. In the higher plants it coagulates at a temperature not much over 50°C. In spores and seeds where the protoplasm is in a dried condition it can withstand a higher temperature. The spores of some bacteria can withstand a temperature 105°C. without being killed.

The Cytoplasm

The soft protoplasm inside the wall and outside the nucleus is designated as the cytoplasm. It is a more or less tenacious semi-fluid. It coheres to the wall completely. The cytoplasm can be separated from the wall artificially by extracting the water from the vacuoles. When this is done it tends to assume a spherical form. The outermost part of the cytoplasm (periphery) is differentiated as a *plasma membrane*. This membrane plays an important role in the passage of water and dissolved substances.

The cytoplasm commonly encloses sap-filled vacuoles and one or more plastids. Other inclusions within the cytoplasm may be raw food materials, stored foods (starch grains, protein granules, oil globules), byproducts or wastes, and crystals.

Certain very small bodies called *mitochondria* or *chondriosomes* are present in the cytoplasm of both plant and animal cells (Fig. 3–5). Formerly they were frequently overlooked because the methods of preparing

[3] W. F. Ganong, *The Living Plant*, Henry Holt & Company, Inc.

microscopic mounts either dissolved them or failed to make them visible. They may be in the form of granules, rods, or filaments. Some investigators believe that they increase by division. Others think that they can arise

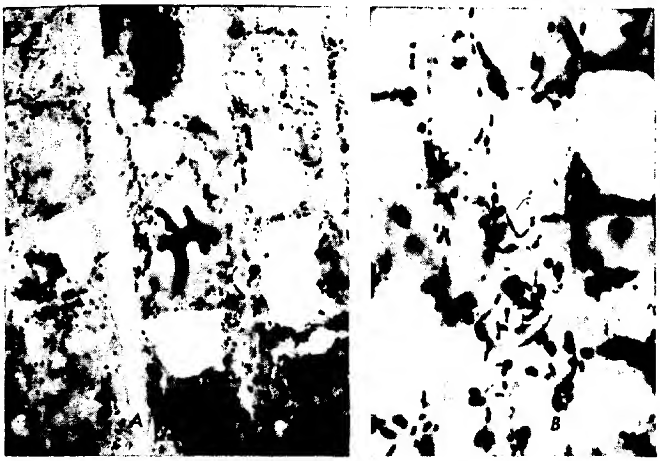


FIG. 3-5. Mitochondria in root tip cells. *A*, in narcissus, the mitochondria appear as small black bodies. The nucleus in the center cell is in a phase of division. *B*, in pea, the mitochondria are forming plastids. (Photographs by E. H. Newcomer.)

in the cytoplasm. There is some evidence to show that they are primordia for plastids and that they later become plastids. It seems probable that the so-called mitochondria are not a single type of body with similar functions but diverse types in both origin and function.

The Nucleus

An important part of the protoplasm of typical plant cells is the nucleus. The protoplasm of the nucleus is usually more dense than the cytoplasm and it also differs chemically from the cytoplasm in the proportion and complexity of its proteins. The nucleus is commonly globoid or ellipsoid in shape and is separated from the cytoplasm by a definite *nuclear membrane*. Within the nuclear membrane are three distinct substances, or structures, namely, the *reticulum*, the *nucleolus* (or nucleoli, if more than one), and the *karyolymph* (Fig. 3-6).

In microscopic preparations the *reticulum* frequently appears as a network of numerous crooked threads. Individual threads or units may not be identifiable in the network of the vegetative or metabolic condition of

nuclei. When nuclei divide, however, changes occur and separate units emerge which are called *chromosomes* (Fig. 3-7). From the facts gained from a study of dividing cells it is evident that the reticulum is a system of associated chromosomal threads. The chromosomes contain a substance

FIG. 3-6. Photomicrograph of a root tip cell of hyacinth. The nuclear membrane is indistinct; the reticulum and two nucleoli, surrounded a clear zone, are evident.

FIG. 3-7. A nucleus of a root tip cell of hyacinth in a phase of division, showing large well-defined chromosomes.

called *chromatin*. Genetic investigations have revealed the fact that they contain a series of basic factors (*genes*) which play an important role in the transmission of hereditary characters from cell to cell and hence from generation to generation. In later chapters further explanations of these important matters will be made.

Vegetative nuclei usually contain one or more *nucleoli*. In the living condition the nucleolus appears as a dull, usually roundish droplet. In prepared slides the nucleolus, as a general rule, appears as a dark staining body surrounded by a clear zone. At the time of nuclear division the nucleoli commonly disappear. The functions of the nucleoli are obscure. Some investigators believe that they are concerned with chromosomal development; others regard them as a reserve of protein material. The *karyolymph*

is a homogeneous substance which forms the larger part of the volume of most nuclei. It is also called the "nuclear sap."

The nucleus as a whole is regarded as the center of the internal physiological activities of the cell. Experiments have been performed in which certain one-celled animal forms (protozoa) have been cut into two pieces in such a way that one piece has the nucleus and the other piece is without it. The piece lacking the nucleus may move about for a time and respond to some stimuli but it gradually exhausts itself and dies. The bacteria and the blue-green algae do not have typical nuclei. In some of them there are materials whose reactions suggest a nuclear nature.

SURVEY OF VARIOUS TYPES OF PLANT BODIES

Large numbers of plants, which at first seem to be quite unlike, actually possess bodies with similar organization of their members. It is possible to determine points of agreement between seemingly different plants and thus simplify the problem. Those who have studied animals know that the vertebrates include a great variety of forms—fish, amphibians, reptiles, birds, and mammals. Yet in this diversity of structure there is a body plan. It is possible to build up a concept of an "ideal" vertebrate body. With this in mind attention may then be given to some of the modifications in the different groups. In like manner there is a "body plan" of the higher plants. Both outer form and inner structure must be considered. It will be best to begin with the simpler types of bodies and then proceed to the more complex ones.

Unicellular Bodies

The simplest form a plant body can have is that of a single spherical cell. There are many such simple plants (Fig. 3-8). A green growth often seen on the north side of trees or old fences consists of aggregations of simple spherical bodies of *Protococcus,* a green alga. Collectively these plants appear as a green stain. Individually the plants are single rounded small cells identifiable only under a microscope. They have firm cellulose walls, a single nucleus, and a dense relatively large chloroplast. These plants may appear as individuals; often, however, they adhere together in groups of two, four, or more cells.

Single plants of ordinary yeast, *Saccharomyces,* are also simple cells, but they are ellipsoidal in shape. They have a peculiar way of budding, and thus often appear to have an outgrowth at the end or side of a cell.

The bacteria, which are well known as the agents of decay and disease, are usually very small one-celled plants. The cells of the bacteria have a variety of shapes. In addition to spherical and ellipsoidal forms there are rod-shaped, filamentous, and spiral forms.

Diatoms are common unicellular plants that form the familiar brown coatings on sticks or stones in sluggish streams or slimy deposits on the bot-

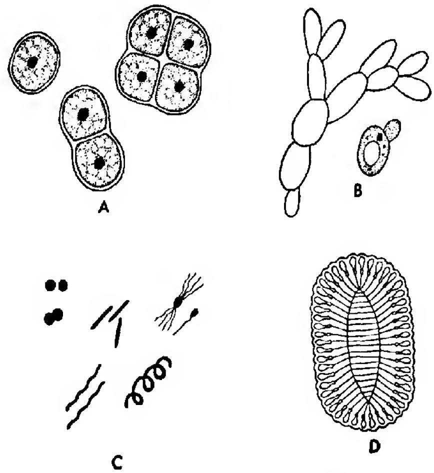


FIG. 3-8. Different types of unicellular plant bodies. *A*, *Protococcus*, a green alga; *B*, *Saccharomyces*, yeast; *C*, various kinds of bacteria; *D*, a diatom. See text for further explanation.

toms of ponds. The individual cells or plants are found in a great variety of forms, some being boat-shaped, others wedge-shaped, helmet-like, or fan-like. Some remain solitary, but others become associated to form bands, ribbons, or zigzag chains. The cells are covered by two glass-like valves, one of which fits over the other like the lid of a box. Because of the silica in them, these valves accumulate on the bottom of ponds and in the sea and in this way form beds of siliceous earth. Earth of this nature is the basis of some polishing powders and is also used as an absorbent in the manufacture of certain explosives.

The blue-green algae are simple one-celled plants that have certain features in common with the bacteria. Some of these algae are readily recognized as unicellular plants, but often the cells are more or less firmly joined together into rows, forming a thread or filament. The filaments

sometimes branch; and this feature, together with the fact that the various cells perform different functions, makes it possible to regard some of these forms not as colonies of individuals joined together, but as multicellular plants.

We have already referred to the plant *Protococcus* as consisting of a single individual cell. There are other related green algae in which the cells are united as definite aggregations or colonies. These colonies may be simple and composed of a few loosely joined cells to form flat discs, or they may consist of many cells in spherical or net-like forms. These aggregations of cells are considered colonies because all of the cells perform the same functions. Groups of cells, some of which are varied in character and perform certain functions not carried on by other cells in the group, may be regarded as constituting multicellular individuals. This brings us to the next stage in the consideration of plant bodies.

Multicellular Bodies of Simple Structure (Thallus Plants)

A simple type of multicellular body consists of cylindrical cells placed end to end to form a thread-like body or filament. The basal cell of a filament may be different in form and serve as a means of attachment. In such an aquatic filamentous green alga as *Ulothrix* (Fig. 3–9) we find this condition. The other cells of the plant are essentially alike, each containing a nucleus and a chloroplast, and are capable of manufacturing food and reproducing. The basal cell does not function thus but serves only to hold the plant fast to some object under water. This sort of cell differentiation is found to a far greater degree in higher plants

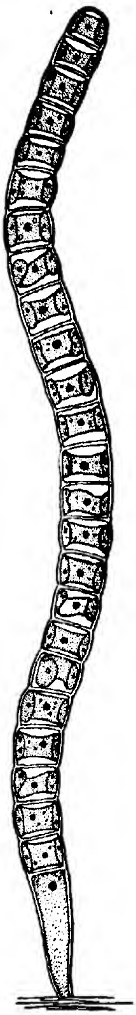


FIG. 3–9. *Ulothrix*, a multicellular plant body consisting of a simple filament. Note that the lowermost cell is modified to serve as a means of attachment.

where there are variations in cells that adapt them to the performance of many special functions.

In the marine green alga known as *Ulva,* division of labor among the cells is carried further by the cells at the base serving for attachment and those at the apex carrying on cell division or growth. Such a plant shows differentiation into base and apex. In the brown alga called *Dictyota* (Fig. 3–10), apical growth results from a large apical cell. Sometimes, following a division, two apical cells continue dividing and the result is a forked (dichotomous) branching.

In the brown and red algae, or seaweeds, there is a high degree of differentiation. The formation of an axis with lateral expanded branches makes many of them appear to possess stem and leaves and even roots. Although there is considerable internal cell differentiation, the resemblance to the higher plants in the formation and arrangement of their parts is chiefly external.

In the mosses and liverworts there is considerable external resemblance to the bodies of the higher plants. While some of them are simple and resemble the algae, others have stem-like and leaf-like structures which parallel the higher plants. But in spite of the apparent variety of external form reached by these plants, their plant body does not attain the complex cellular organization of the higher plants and is called a *thallus.*

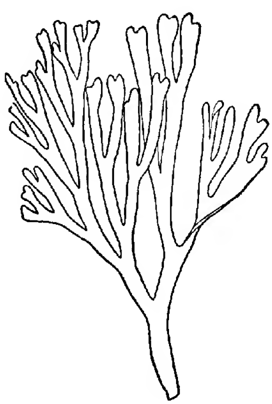


FIG. 3–10. *Dictyota,* a brown alga, illustrating forked (dichotomous) branching. (After Oltmanns.)

The simpler liverworts have a flat thallus which grows prostrate upon the earth (Fig. 3–11). By the division of the apical growing cell into two parts, already described in *Dictyota,* there are formed two growing points which produce a dichotomous branching. On the under side of the thallus numerous filaments (*rhizoids*) grow into the earth and serve both for attachment and for the absorption of water. The flat thallus is green. The upper cells bearing the chloroplasts are loosely arranged. Small pores permit a circulation of air so that the conditions for photosynthesis are provided. The lower cells do not develop chloroplasts and doubtless serve for food storage.

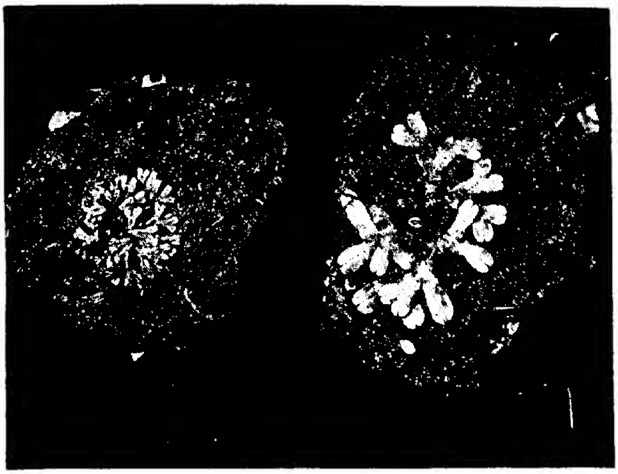


FIG. 3-11. One of the liverworts with a flat thallus which has forked (dichotomous) branching.

FIG. 3-12. Two plants of *Sphagnum* moss showing stem-like axis and radially arranged leaves.

The mosses generally have a stem-like axis with radially arranged leaf-like structures and root-like rhizoids below (Fig. 3-12). The cells show considerable differentiation. An advance over many of the liverworts is a central strand in the axis of some mosses which serves to conduct water. Although organs for absorption and conduction of water are present, they do not function effectively enough to permit moss plants to attain any considerable height. Many mosses are creeping forms and those that are erect rarely grow more than a few inches in height.

Multicellular Bodies of Complex Structure (Vascular Plants)

The vegetative body of ferns and seed plants consists of two main parts: a *green shoot system,* divisible into stem and leaf, which usually grows above ground, and a *non-green root system,* which nearly always grows underground. (See Fig. Introd.-1.) These two parts of the plant body are adapted to two very different sets of conditions. The *shoot* carries on photosynthesis where light and carbon dioxide are available in the atmosphere above, and the *root* absorbs water and minerals from the soil underneath.

Because of the similarity of organization of ferns and seed plants, it may be assumed that they have had a common origin and that their similarities are due to true relationship. However, our concern is not to trace out relationships but rather to become familiar at first with the main external and internal structures of the primary members of the plant body. After this, some attention must be given to the variations and modifications of these parts. Sometimes the modifications are so extensive as to result in one primary member assuming the character or functions of another.

The Shoot

Under the term shoot is included a stem and its leaves and flowers. The stem may be a simple axis or it may be branched. Branches develop from the upper angle between a leaf and the stem (*axil*). Therefore, the arrangement of branches is dependent upon the arrangement of the leaves. Leaves are always borne according to a definite plan.

Arrangement of Leaves. The places on a stem where leaves arise are called *nodes,* and the regions between the nodes are known as *internodes.* In some stems, such as the familiar bamboo, the nodes are prominent and easily seen even after the leaves have fallen or been removed. In many stems there is not much enlargement at the nodes, or other external evidence of their position except the presence of a leaf, or a leaf scar if the leaf has fallen. The term *phyllotaxy* is used to refer to the manner in which leaves are arranged on a stem axis. (See Fig. 3-13.)

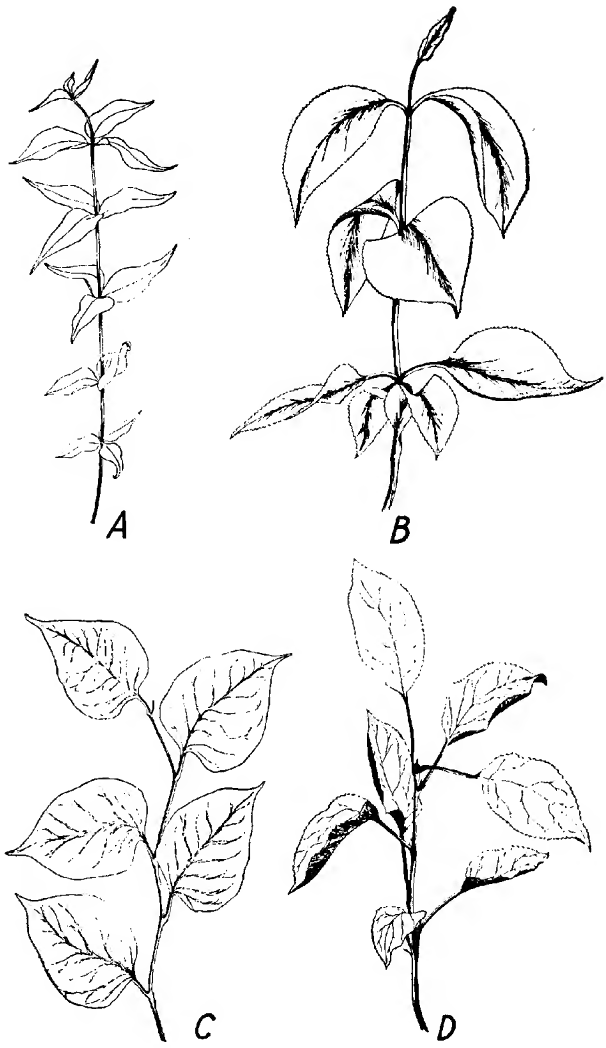


Fig. 3–13. Types of phyllotaxy. *A*, whorled; *B*, opposite; *C*, alternate with 1/2 arrangement; *D*, alternate with 2/5 arrangement. (Drawings by Elsie M. McDougle. Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

In some plants a single leaf is borne at a node. This is called an *alternate* arrangement. In other plants there may be two leaves at a node, each on opposite sides of the stem. This arrangement is known as *opposite*. Some plants have three or even more at a node. These are known as *whorled* arrangements.

When leaves are alternately arranged the attachment at any node is not directly above that of the node below but to one side. The distance around the circumference between the attachment of two successive leaves varies in different plants but it is always uniform in the same plant. The greatest separation is one-half the circumference; it occurs in corn, iris, spiderwort, and basswood. Another separation is one-third the circumference; it is found in sedges and in white hellebore. A more common divergence between two successive leaves is two-fifths of the circumference; this is seen in apple, cherry, and many other trees and shrubs. Such an arrangement is a spiral one. The sixth leaf is above the first, the seventh above the second, and so on. Still other fractional divergences are 3/8, 5/13, 8/21, and 13/34. Here we have a new way of adding fractions, for it will be observed that in each fraction the numerator and denominator are the sums of those in the two preceding ones. The 2/5 arrangement follows the 1/2 and 1/3. It will also be noted that, in tracing the spiral, the numerator represents the number of turns around the stem in going from a leaf to one exactly above it. The denominator represents the number of leaves, or, to put it somewhat differently, the number of vertical rows of leaves on the stem.

Why there should be such systems of leaf arrangements is obscure, but it is obvious that definite and symmetrical arrangements do produce certain advantages. The distribution of the weight of the leaves is even, and if the stem is upright the leaves have equal opportunities for the utilization of light.

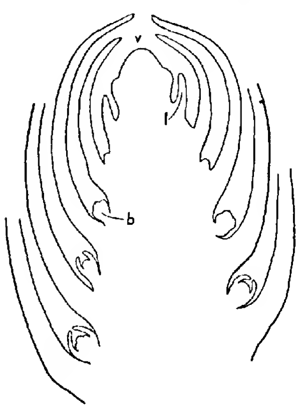


FIG. 3-14. Lengthwise section of the apex of a shoot showing the vegetative cone (v), the rudiments of leaves (l), and axillary buds (b).

Buds and the Development of the Shoot. It has been pointed out that the term shoot includes a stem and its leaves. The apical end of the stem is the growing point. The actual apex is usually too small to be seen by

the unaided eye but when magnified it appears more or less cone-shaped and has been called the *vegetative cone.*

As the vegetative cone of the stem grows, the developing leaves appear first as little conical protuberances. The nearer the tip the smaller are these protuberances, and the farther away the better developed they appear (Fig. 3-14). Since the leaves farther back develop more rapidly than the embryonic stem which produced them, they come to overarch the vegetative cone. This vegetative cone thus protected is a *bud.* In other words, a bud is merely an undeveloped shoot.

New buds have their origin as protuberances in the axils of the embryonic leaves of the vegetative cone. By *axil* is meant the upper angle which the leaf makes with the stem. In its turn this axillary rudimentary growth develops into an *axillary* bud. These axillary buds, because they appear on the side of the stem, are termed *lateral* buds, in contrast to the bud at the upper end of the stem, which is called a *terminal* bud. Development of a terminal bud continues the growth of a stem in length; development of axillary or lateral buds causes a branching of the shoot. In contrast to the lateral and terminal buds which are always in fixed positions, some buds are in irregular positions. They may occur on roots, leaves, or on the internodes of stems. These are called *adventitious* buds.

Sometimes terminal growing tips continue the development of a shoot for a long time without the development of an outer covering of scales. As a means of protecting the vegetative cones from drying out they are usually invested during the resting period with tough scale-like leaves known as *bud scales.* These bud scales may be rendered more waterproof by gums, resins, or hairy coatings. In temperate latitudes the resting or dormant buds of the winter are always covered with scales. On many shoots in winter condition the lateral buds can be readily seen just above the leaf scars. Even most tropical plants must withstand a dry period; hence their buds are likewise protected by scales. When the scales of a (terminal) bud drop off they often leave characteristic ring-like scars about the stem. By means of these we can tell where the growth of one season begins and ends (Fig. 3-15). In woody plants in which the terminal bud lives through the winter it starts a vigorous growth in the spring. Ordinarily all of the lateral buds do not develop, but some of them may do so if the terminal is pruned off or if it is injured by insects or by frost. Lateral buds which do not develop may remain in position for a long time.

General Features of Leaves. Leaves vary so much in shape and size that it is difficult to make any statements that are generally descriptive of them. We may be safe in saying that green leaves are the most conspicuous parts

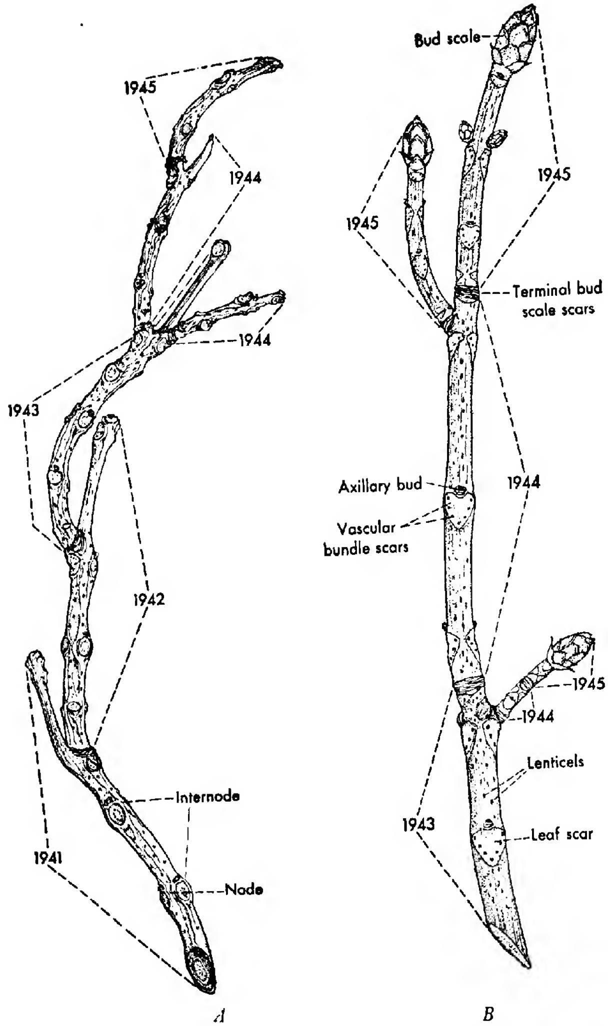


FIG. 3-15. *A*, shoot of catalpa showing continuation of growth by lateral buds; *B*, horse chestnut in which growth is continued by terminal buds.

of the vegetative plant body. We can agree that it is hardly an exaggeration to describe the green leaf as one of the most wonderful things in the world. The work which it does provides the store of carbohydrates, and the more complex nitrogen-containing proteins, on which practically the whole organic world subsists.

The great majority of foliage leaves are thin, flat organs. The flat expanded portion is the *blade*. The blade may be attached directly to the stem or it may be borne on a stalk called the *petiole*. Sometimes at the base of the petiole where it joins the stem there is a pair of appendages called stipules. A complete leaf consists of *blade, petiole,* and *stipules*.

Examination of leaves in good light reveals that there is an elaborate system of veins in the leaf blade. On the lower surface the larger veins project more or less to form definite ribs. In many leaves there is a central large vein or midrib from the petiole to the tip. This gives off strong lateral branches which reach nearly or quite to the margins. Between the lateral branches are smaller branches which are still further subdivided until slender veinlets ramify throughout the blade. The smallest veinlets can be seen better with the aid of a magnifying glass. The venation of a leaf may be best appreciated by observing one in which the softer tissues have weathered away, leaving only the skeleton composed of the veins (Fig. 3–16).

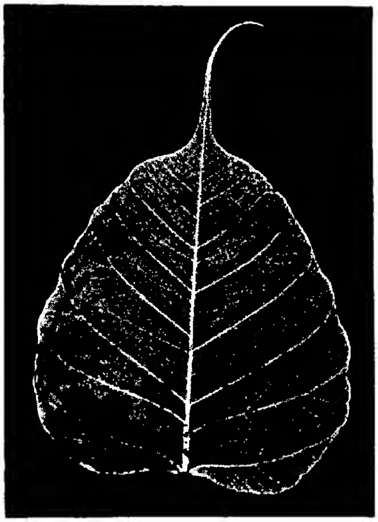


Fig. 3–16. Photograph showing the system of veins in a leaf—midrib, lateral veins, and network of veinlets. This specimen bears a scene painted by a Chinese artist.

The veins serve a dual purpose. The stronger ones form a mechanical framework and the whole branching system acts as a conducting system. The conducting is of two kinds, one for the distribution of the water which has come through the stem from the roots, and the other for the distribution of the food which is manufactured in the green cells of the leaves.

Leaves are often classified on the basis of their venation system. In general there are two sorts, *parallel-veined* and *netted-veined*. In the parallel type the large veins are about equal in size (except for a possibly larger midrib) and run more or less parallel from the base to the apex. These larger parallel veins may be united by smaller cross veins. We have already described a netted-veined leaf of the pinnate type—called pinnate because there is a prominent central vein with lateral branches on either side like the arrangement of the shaft and barbs of a feather. Another type of netted-

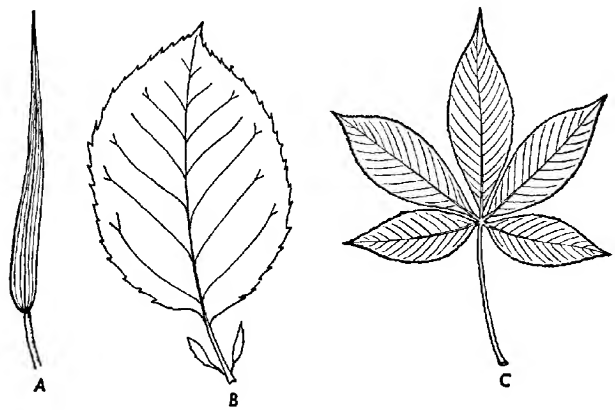


FIG. 3-17. Three types of venation. *A*, parallel; *B*, pinnate; *C*, palmate. The latter is a compound leaf, the others are simple. *B* is a complete leaf with blade, petiole, and stipules.

veined leaf is that known as *palmate*—called palmate because there are several equally prominent veins branching outward from the point of attachment to the petiole and resembling an open hand. (See Fig. 3-17.)

Reference has been made to the great variations in the forms of leaves. Variations may be due to the shape or length of the petiole. The petiole may be absent and the leaf is then said to be *sessile*. Whether stipules are present or not, their shape and size, if present, result in variations. But the greatest variations are found in the blades. Size, shape, margin, texture, and surface are all variable. This account cannot be complete enough to do justice to the subject, but we would fail if we did not present some variations.

To describe the shapes of leaves a good many terms are used by systematic botanists, who make it their business to write careful descriptions of plants. Here are some of the descriptive terms (see Fig. 3-18): *linear*

(narrow and elongate), *lanceolate* (lance-shaped), *elliptical* (oval), *ovate* (egg-shaped), *cordate* (heart-shaped), *peltate* (shield-shaped), and *sagittate* (like an arrowhead). The margins of the blades (Fig. 3–19) may be unbroken and are then said to be *entire.* Often they are toothed with the

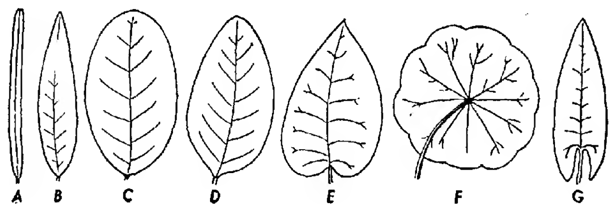


FIG. 3–18. A series of shapes of leaves. *A*, linear; *B*, lanceolate; *C*, elliptical; *D*, ovate; *E*, cordate; *F*, peltate; *G*, saggitate. (After Gray.)

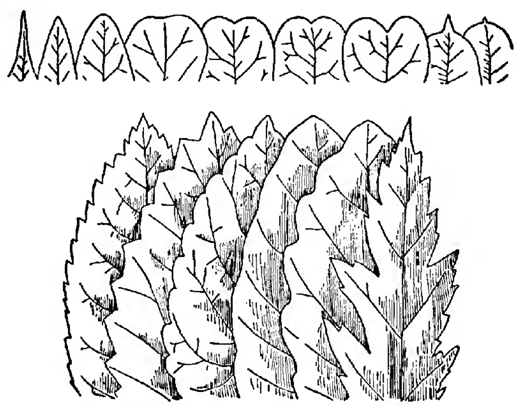


FIG. 3–19. Forms of the apex (above) and of the margins of leaves. (After Gray.)

teeth pointing outward, *dentate,* or with the teeth pointing forward, *serrate.* Or the margin may be *wavy* or *lobed* or *indented.* If the blade is in one piece even though deeply indented, the leaf is said to be *simple.* If the indentations are so deep as actually to divide the blade into separate parts (*leaflets*), the leaf is *compound.* Either the pinnate or the palmate leaves may be compound. A pinnately compound leaf has two rows of leaflets along a common axis (*rachis*). A palmately compound leaf has several leaflets radiating from the petiole. The number of leaflets in either type

may vary greatly. The leaflets in turn may be compound so that leaves may be twice-compound or even thrice-compound. A single leaflet of a compound leaf may resemble very closely in form a simple leaf of another plant, but it must be kept in mind that such a leaflet is not growing out of a stem and does not have a bud in its axil. The leaflets in turn may be variously shaped and the margins may be entire or broken as is the case in simple leaves.

The great variation of leaves in shape and margin has caught the interest of some literary folk. A poet has offered the fanciful explanation that originally "the leaves on the trees were as one; they were round, just as round as the sun" and he then proposes in further rhyme that the woodland spirit Pan carved them into strange figures by nocturnal clipping and snipping. He writes:

> One tree was entangled
> With stars five-angled—
> The sweet-gum, towering and gray;
> And another was spangled
> With ribbons that dangled—
> The sandbar willow today!
>
> Some were given a trim
> Of the merriest whim—
> Sassafras, tulip and haw,
> And some looked a bit grim
> As they swung on their limb
> For their edges were notched like a saw.[4]

The Root

Ordinarily the root is an underground structure and serves to attach the plant firmly to the soil. Other important functions are the absorption and conduction of water and dissolved soil minerals and the storage of manufactured foods. The root system may vary in appearance according to its adaptation for the performance of one or the other of these functions. We shall pay attention first to the form and structure of roots adapted to the usual functions of anchorage and absorption.

General Features of Roots. When a seed germinates, the primary root usually grows directly downward. If it continues as the principal root of the system it is termed the *taproot.* Secondary branches arise from the side

[4] From Paul Southworth Bliss, *How Pan Shaped the Leaves and Other Poems.* Copyright 1931 by Paul Southworth Bliss.

of the primary and these branches may in turn give rise to other lateral branches. Since roots do not have leaves and nodes, the lateral branches do not make their appearance at regular intervals up and down the parent root. The lateral branches do appear, however, at regular intervals around the parent root or, in other words, in longitudinal ranks or rows. There are in some roots four equidistant rows of branches, but the actual number of rows is dependent upon the internal structure of the parent root. A branch root has an internal origin and must grow through certain overlying tissue before it appears on the outside.

In some plants numerous adventitious roots develop about the base of the stem and there is no main root or taproot. Most grass plants have this sort of fibrous root system. In other plants there is a condition in real contrast to this, for there is not only a taproot but it is much enlarged for food storage, making the lateral branches seem very insignificant. Radishes and turnips have such fleshy taproots.

The Structure of Young Roots. The expression "young roots" refers either to the short root of a seedling or to the tip portion of an older root system. Since roots have apical growth the tips are the younger parts. All the absorption of water takes place through these younger, delicate parts of the root system. When we learn how much water the roots of a large tree absorb from the soil

FIG. 3–20. Root system of a tobacco plant showing the extent of development. This specimen was grown in a water culture. It is difficult to obtain views of root systems of plants growing in soil because of the tendency of the smaller branches to break off in the process of separation.

in a day, it may seem impossible that it is all accomplished by the portions within a few millimeters of the tips, but this is the case. It is difficult to realize how profusely branched the root system may be and so we cannot appreciate readily how many young tips there are (Fig. 3–20).

The actual apex, or vegetative cone, of the young root is covered with a thimble-like protective layer of cells known as a *rootcap.* Since the growing tip of a root is forced through the soil as the root elongates, the rootcap

functions in a real way to protect the tender cells which it covers. The cap itself is worn away on the outside but it is renewed by new cells forming within so that it maintains itself as it is pushed downward. On the roots of most of our common plants the rootcaps can be seen only when magnified, but on aerial roots of some tropical plants they are plainly visible. The growing tip of stems is not sheathed with any structure at all similar to the rootcap.

To the unaided eye the small tip looks whitish for several millimeters and is in general cone-shaped. This region is the growth zone where cells are dividing and elongating. Just above this region there can be seen a narrow zone in which fuzzy whitish hairs radiate from the young root (Fig. 3-21). There is a multitude of these *root hairs.* Nearer the tip they are younger and shorter and farther back they are older and longer (Fig. 3-22). If seeds are sprouted in moist air

Fig. 3-21. Seedlings of mustard showing growing tip and root hair zone above.

between damp papers, the smooth tip and the root hairs can be seen as described. When roots are removed from the soil and washed, the hairs usually will be torn and injured because they are so delicate. Even those

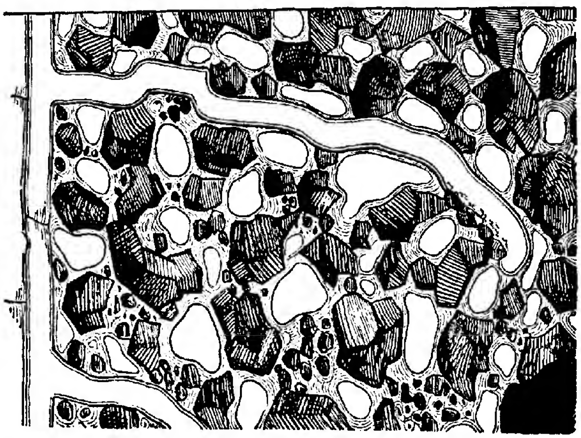


Fig. 3-22. Diagram of root hairs among particles of soil (darkly shaded), air spaces (white), and soil water (concentric lines). (After Sachs.)

grown between moist papers, as just suggested, must be examined promptly and carefully because a few moments in dry air causes them to collapse.

Dr. Oliver Wendell Holmes was much impressed with the activity of the roots of plants. In "Over the Teacups" he said, "A tree is an underground creature with its tail in the air. All its intelligence is in its roots. All the senses it has are in its roots. Think what sagacity it shows in its search for food and drink! Somehow or other, the rootlets . . . find every crack in the rocks where there are a few grains of the nourishing substances they care for, and insinuate themselves into its deepest recesses. . . . The next time you see a tree waving in the wind, recollect that it is the tail of a great underground, many-armed polypus-like creature. . . ." This figurative description places deserved emphasis on the importance of the root system.

CHAPTER 4

THE INTERNAL STRUCTURE AND DEVELOPMENT OF VEGETATIVE ORGANS

(*Anatomy, Growth*)

We have already considered the gross features of stems, leaves, and roots; but in order to understand how the whole living structure works we must learn about the inner organization of the parts. If we knew only that a house had in it living room, dining room, kitchen, bedrooms, and bath, but knew nothing of the furniture and equipment or how the rooms were connected, we would be in a poor position to know whether it was well adapted for the purposes of a dwelling. Likewise we must know how the organs of the plant are "furnished, equipped, and connected," if we wish to understand its activities.

TISSUES

The bodies of the higher plants are composed of countless numbers of cells. Microscopic examination of the apex of stems or the tips of roots (vegetative cones) reveals that all the cells are essentially alike in form and structure. But examination of the older parts of stems and roots reveals that the cells are not by any means all alike. The plant body is a complex structure composed of groups of cells called *tissues*. There are many different kinds of tissues, differing in the character of the cells and differing in the functions they perform. *Simple tissues* consist of groups of cells having essentially the same structures; *complex tissues* are composed of several kinds of cells. Tissues may be grouped as *tissue systems* on a functional basis.

Kinds of Tissues

We have referred to the cells in the apex of stems and roots. There are regions in which the cells are engaged in dividing and producing more cells (see Fig. 3-2). These apical tissues are undifferentiated or *embryonic* tissues. The botanical term for an embryonic tissue is *meristem*. Contrasted to these embryonic or meristematic tissues are the mature tissues. The plant

body consists chiefly of mature tissues. There are conductive tissues where the cylindrical cells are adapted to conducting water or distributing food. Other good examples are the strengthening or mechanical tissues where the cells have thick stout walls which give strength and support (see Fig. 2-5). In the leaves are *food-making* tissues where the cells are characterized particularly by green plastids.

Tissues may be designated by common names based on their functions. We have already referred to conductive, mechanical, and food-making tissues. There are also absorptive, storage, reproductive, and protective tissues. It should be understood that such designations are purely general and that they in turn may be subdivided. For example, conductive tissue for *water* is quite different structurally from tissue that is conductive for *food*. Also the kinds of cells which form the conductive tissue for water may be different in one kind or group of plants from those in another group of plants. Neither is it possible to look upon a tissue as devoted only or even chiefly to a single function. No method of classifying plant tissues has been proposed which is not open to some objection.

The meristem tissues give rise to the complex structure of the plant through division of their cells followed by enlargement and differentiation. A meristematic cell as it progressively differentiates may be only slightly changed or very greatly changed, depending upon the kind of tissue of which it becomes a part. Ordinarily tissues do not increase by division of their own cells but by additions from the cells of meristematic regions. Under certain circumstances some tissues revert to a meristematic condition and produce tissues quite unlike themselves.

It is a familiar fact that stems and roots may grow both in length and in diameter. The growth in length is brought about by apical or terminal meristems known as *primary tissues*. The increase in diameter is accomplished by the activity of meristems located laterally, and the tissues thus formed are *secondary tissues*.

To continue our considerations of the internal anatomical structures until we became familiar with all the possibilities and variations would carry us too far. But we must pursue our studies far enough to get a clear picture of how cells are grouped to form tissues and how tissues are grouped to form systems and organs. It is an excellent concept that "we may picture the healthy, living plant as a marvelously constructed body, in which there is a splendid division of labor, with all cells, tissues, and organs working in harmony." We should also come to realize that living organisms resemble each other not only in gross structure and function, but in microscopic structure as well.

Tissue Systems

Tissues are united in the body of a plant to form tissue systems. Stems, leaves, and roots are commonly referred to as the vegetative organs. A leaf is covered with a protective tissue, and has conductive and mechanical tis-

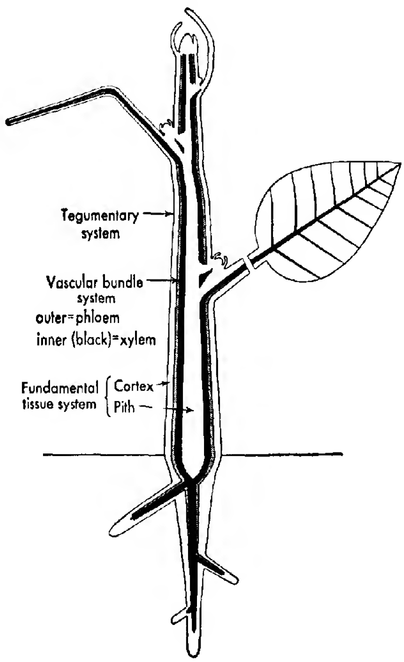


FIG. 4–1. Diagram showing arrangement of the three tissue systems.

sues in its veins, and food-making tissue in its softer parts between the veins. The protective tissue of the leaf is continuous with the protective tissues of the stem and root; the conductive and mechanical tissues of the veins of the leaf are continuous with and form part of a conductive and mechanical system in the stem and root; the food-making tissues of the leaf are continuous with and part of the basic internal tissues of the stem and root. Here may be distinguished three *tissue systems:* (1) the *tegumentary system* (protective), (2) the *vascular bundle system* (conductive and mechanical), and (3) the *fundamental tissue system* (chiefly nutritional but also mechanical); see Fig. 4–1. The fundamental system is enclosed by the tegumentary system

and traversed by the vascular system. This concise statement expresses the facts very well. From this general conception of the manner in which these tissue systems comprise the body of the plant, we may turn to the structural features of the organs, leaves, roots, and stems, in order that we may understand the particular parts they play in the life of a plant. Our conceptions can be correct and clear even if our considerations are too brief to be complete.

Leaf Tissues. The tegumentary system of the green leaf consists of a colorless single layer of cells called the *epidermis.* The function is distinctly protective. The soft internal cells would quickly dry out in the sun and wind if they were not protected. The outer walls of the epidermal cells are overlaid with a waxy material known as *cutin.* The layer of cutin is called the *cuticle.* The cuticle is not wholly waterproof but it is sufficiently impervious to the passage of water and water vapor greatly to reduce water loss from the interior cells by evaporation. The cuticle is continuous over the surface of the epidermal cells.

If the epidermal cells were close together without any intercellular breaks, water loss from within would be checked, but the passage of the atmospheric gases, carbon dioxide and oxygen, to and from the internal cells would be prevented. There are extremely minute openings in the epidermal layer called *stomata* (singular, *stoma;* the terms *stomates* and *stomate* are also used). A stoma is a slit-like opening between two special epidermal cells termed *guard cells* (Fig. 4–2), which permits movement of gases between the atmosphere and air spaces within the plant body. The guard cells differ from the other epidermal cells in their shape, structure, and contents. They are kidney-shaped or, as has been stated, they "may

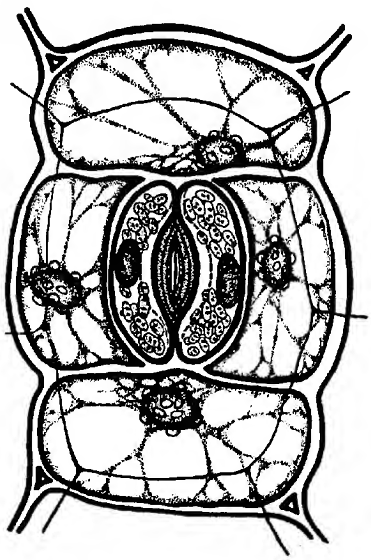


FIG. 4–2. Surface view of a stoma, with guard cells containing nuclei and chloroplasts, and neighboring epidermal cells containing nuclei, leucoplasts, and cytoplasmic strands. (Drawing by Louise Burpo.)

be compared with a couple of miniature sausages placed side by side, stuck together at the ends then pulled apart in the middle so that an oval space is left" between them. The walls facing each other are thicker than the remainder of the walls. The guard cells contain chloroplasts which are commonly lacking in the ordinary epidermal cells. Stomatal reactions are the indirect response of the guard cells to light (Fig. 4-3). In the light a series of chemical and physical processes are initiated which increase their volume, resulting in greater curvature and enlargement of the open-

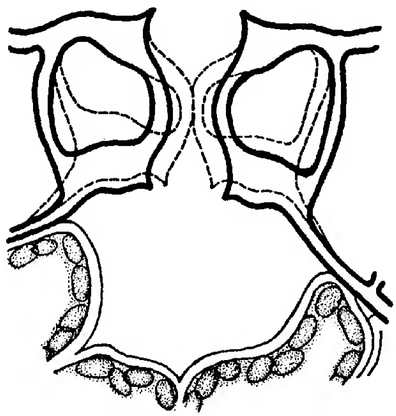


FIG. 4-3. Sectional view showing how the guard cells open and close the stoma through changes in shape.

ing. The opposite effects are brought about in darkness. Because these two special cells on the sides of the stoma thus vary the size of the opening they have received the name of *guard* cell. This is a brief description of what may be termed the stomatal mechanism. A good way to observe much of what has been described is to strip off a bit of epidermis, mount it on a glass slide in water under a cover slip, and examine it under a microscope. The under surface of a leaf of the Wandering Jew lends itself well to such a study.

As a rule more stomata are found on the under side of leaves than on the upper side and in some plants they are confined to the lower side. The number of stomata varies in different plants from a few up to 500 to 600 or more per square millimeter of surface. It is estimated that there may be an average of about 125,000 per square inch in many common leaves.

Hairs or scales, called *trichomes,* are characteristic of the tegumentary

system. The epidermal hairs may consist of a single cell, or they may be multicellular; either simple rows of cells or branched structures. Sometimes they are disc-shaped or star-shaped. The cells of some hairs retain their protoplasm; others die and become filled with air. Dead hairs are common on the leaves of many plants. The stinging hairs of nettles contain poisonous contents.

The internal fundamental tissue of a leaf is termed *mesophyll.* The cells have thin walls and numerous chloroplasts. The mesophyll is the great

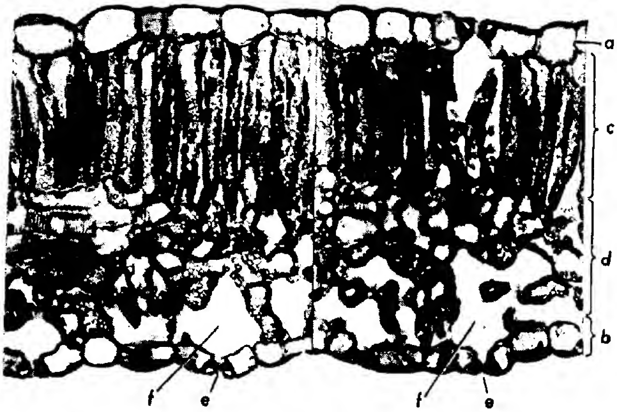


FIG. 4–4. Photomicrograph of a cross section of a leaf showing upper epidermis (*a*), lower epidermis (*b*), palisade layer (*c*), spongy mesophyll (*d*), and stomata (*e*), opening into intercellular air spaces (*f*).

food-making tissue. In many leaves the cells on the upper side are longer than broad and are arranged closely side by side in a palisade-like manner; because of this arrangement they have been called the *palisade layers.* The cells on the lower side are shorter and loosely arranged with many large intercellular spaces giving a spongy effect; because of this appearance they have been termed the *spongy layers.* These facts are brought out best by studying a cross section of a leaf prepared for microscopic examination (Fig. 4–4). In such a section it is possible to observe also how the stomatal openings communicate with the intercellular spaces which form a connected aeration system whereby every mesophyll cell is brought into communication with the external air. There is no apparatus for forcing a flow of air similar to the inhalation or exhalation of air in the lungs of animals. The passage of gases is a purely physical phenomenon resulting from the natural tendency of all gaseous molecules to diffuse, i.e., to dis-

perse from regions of abundance to regions of scarcity. When carbon dioxide is used by the mesophyll cells, its concentration in the intercellular spaces becomes less than in the outside air and some molecules pass through the stomata if they are open. If the stomata are closed, the

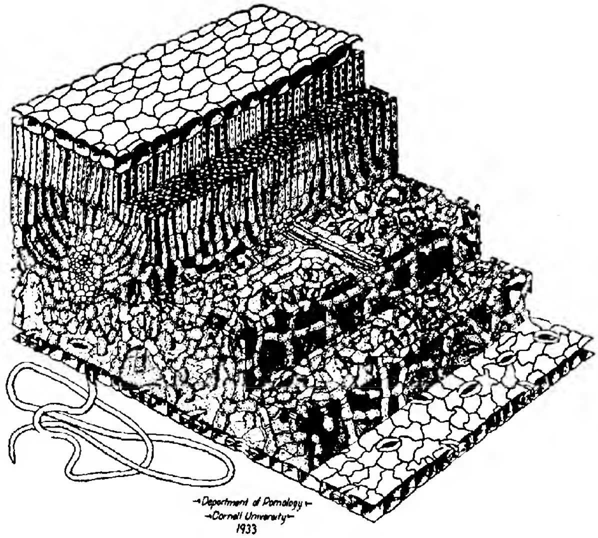


FIG. 4-5. Three-dimensional diagrammatic drawing of a portion of an apple leaf showing arrangement and interrelation of cells. Note that a vein is shown in cross section and also in lengthwise section; one elongated trichome appears growing from a cell of the lower epidermis. (Drawing, courtesy L. H. MacDaniels. From *Cornell Memoir 258*, Cornell University Agricultural Experiment Station.)

passage of the molecules is retarded or prevented. Ordinarily the stomata are open during the day and closed, or partially closed, at night.

In a cross section of a leaf it should be possible to gain a partial idea of the vascular bundle system, because the section nearly always cuts through a vein. Since the veins run in various directions we may find a place where a section parallels a vein and gives us a longitudinal view, or another place where it cuts across at a right angle and gives us a transverse view. Through a study of the two views (Fig. 4-5) it is possible to determine both the arrangement of the tissues and the character of the cells. A vein is in reality a single *vascular bundle* (Fig. 4-6). There are two kinds of conducting tissues, *xylem* (water-conducting) and *phloem* (food-conducting). The transverse view shows that these two tissues lie side by side, the xylem

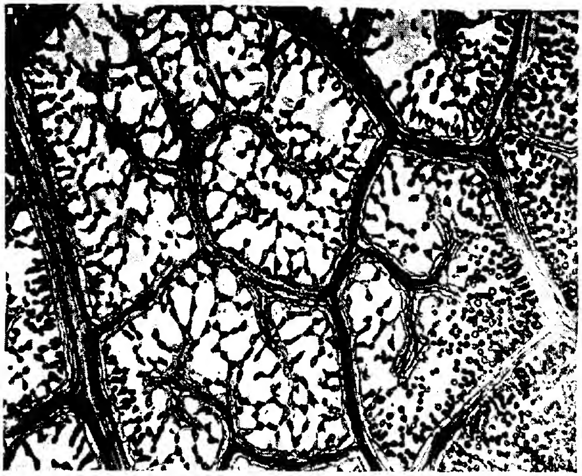


FIG. 4-6. Section parallel to surface of leaf showing spongy mesophyll, branching veins, and bundle ends. Photograph by L. H. MacDaniels, From *Cornell Memoir 258*, Cornell University Agricultural Experiment Station.)

toward the upper side of the leaf, and the phloem toward the lower side. The xylem consists of elongated cells and tube-like vessels which may be called tracheary elements. These elements appear hollow because the protoplasmic contents have disappeared. The movement of the water to the mesophyll occurs chiefly in these tracheary elements. In the larger veins there are several parallel strands of vessels; in the smaller veins there are fewer strands. The walls of the tracheary cells frequently have thickenings which wind around in a spiral manner (Fig. 4-7). Breaking a petiole of geranium leaf and separating the pieces carefully will pull the spiral thickenings from the vessels so that they can be readily observed. Sometimes the thickenings are in the form of a network rather than a spiral. Vertical series of cells may be

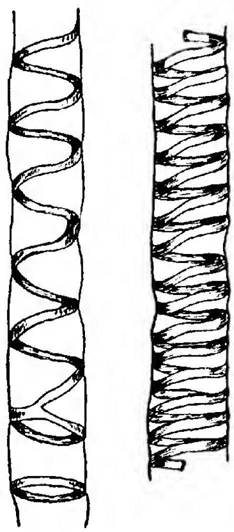


FIG. 4-7. Tracheary elements strengthened on the inside by spirals. (Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

joined in chains with the end walls missing or perforated so that they form tubes. Such elements are called ***vessels*** or ***tracheae***. Individual elongated cells are called ***tracheids***. As the veins become smaller by branching, the number of tracheary elements in them becomes fewer until the tips may be composed of a single tracheid (Fig. 4-8). The veins with their smaller and smaller branches penetrate all parts of the fundamental food-making tissue so completely that no mesophyll cell is more than a few cells away

FIG. 4-8. The anchor-shaped bundle tip is an enlargement of a portion of Fig. 4-6. (Photograph by L. H. MacDaniels. From *Cornell Memoir 258*, Cornell University Agricultural Experiment Station.)

from a conducting element. This arrangement facilitates conduction of water to the photosynthetic mesophyll cells and provides an outlet for the sugars made by them.

The phloem, or food-conducting part of a bundle, has cells which are small in comparison with the xylem cells. They contain protoplasm and the walls are thin. More than one type of cell can be distinguished. The more conspicuous ones are elongated and arranged more or less definitely end to end in longitudinal rows. These cells form a series by the connection of their protoplasm through small perforations in thin areas which are called ***sieve plates***. The cells are called ***sieve tubes*** (Fig. 4-9). Sieve plates are common in the end walls but may occur also in the side walls.

In the main veins there are usually mechanical tissues, in the form of fiber-like cells, surrounding the xylem and the phloem and called the

bundle sheath. The thickness of the sheath varies with the size of the vein. Sometimes a sheath is not continuous around the bundle and the fibers are restricted to strands on the upper and lower sides.

A petiole has an epidermis surrounding a considerable mass of fundamental tissue. There are usually several separate vascular bundles which are branches from the vascular system of the stem and continuous with the veins of the leaf blade. They are often arranged in the form of a semicircle as seen in cross sections or in the scars on the stem after the leaves have fallen.

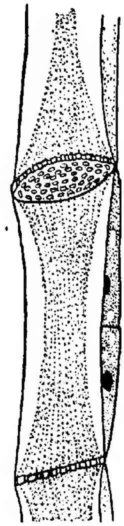
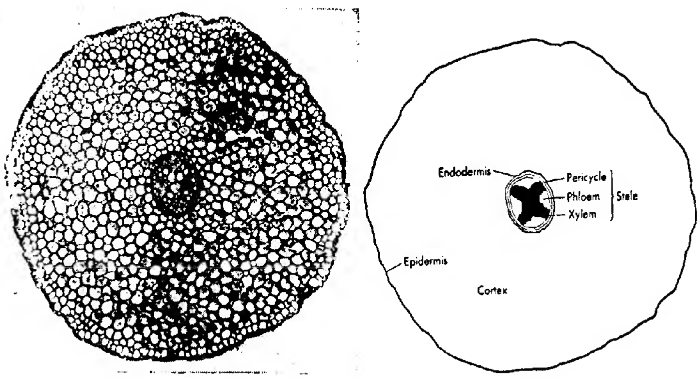


Fig. 4–9. A sieve tube of the phloem showing the end walls perforated to form sieve plates; the smaller cells on the right are companion cells.

Root Tissues. A transverse section of a young root taken from the region a little above the root hair zone, where the cells have all reached maturity, is excellent for the study of tissue arrangement. Here only primary tissues are present. This means that all the tissues are developed from the meristem of the root tip. Three regions comprising the three tissue systems, tegumentary, fundamental, and the vascular bundle, are readily recognizable: (1) the *epidermis*, (2) the *cortex*, and (3) the *stele* (vascular cylinder); see Fig. 4–10.



A *B*

Fig. 4–10. *A*, photomicrograph of a cross section of root of *Ranunculus* (buttercup) above the root hair zone; *B*, diagram of same to show location of tissues.

The epidermis of young roots is a single layer of cells. From the epidermal cells just above the zone of elongation in the root tip root hairs develop. A root hair is a tubular outgrowth from the outer wall of an epidermal cell (Fig. 4–11). The hairs have thin cellulose walls. The hairs are short-lived, but as the older ones above collapse and die new hairs form below. Thus the zone of root hairs remains about the same width. As the root elongates, the root hair zone moves along at the same rate—it is always about the same distance back of the tip—so that new ground is being invaded constantly during the growing season. Because there are so many hairs in such a small zone a large absorbing surface is provided. It is estimated that the hairs increase the absorbing area from five to twenty times. It is through the root hairs that the chief supply of water and mineral salts is obtained.

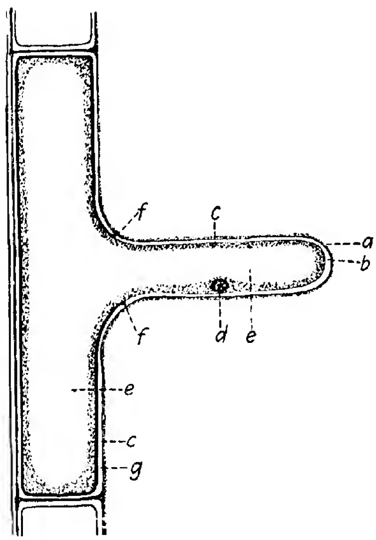


FIG. 4–11. Diagrammatic lengthwise section through a root epidermal cell showing origin and structure of a root hair; *a*, outer wall layer; *b*, inner wall layer; *c*, peripheral cytoplasm; *d*, nucleus; *e*, vacuole; *f*, point where root hair burst through the cellulose layer; *g*, cellulose layer. (Drawn by F. Brown. Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

The cortex is an extensive region comprising most of the bulk of the root. The stele is centrally located and relatively small. The cortex extends from the epidermis to the *endodermis,* a definite sheet of cells, one layer thick, surrounding the stele. The cortex is composed of living colorless cells which are not greatly different from the cells of the meristem except that they are larger. They may be close together or sometimes they may allow considerable intercellular spaces. Such relatively undifferentiated cells as these in the cortex of the root are called *parenchyma cells;* they may be found in many regions of the plant.

The outermost layer of cells of the stele, or central cylinder as it is often called, is the *pericycle.* The xylem portion of the stele which is central in many kinds of roots appears in cross section to radiate like the points of a

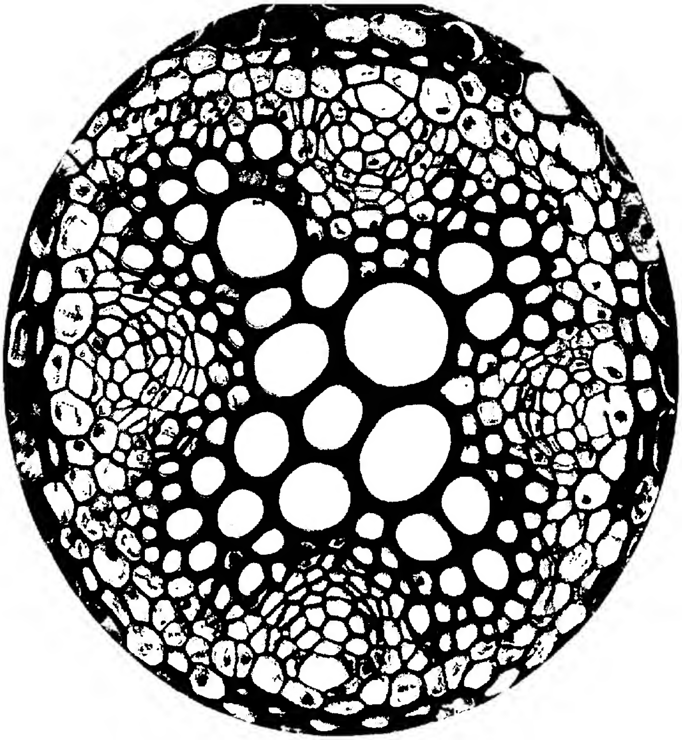


FIG. 4-12. Cross section of root of *Ranunculus* showing the stele, or central cylinder. The thick-walled red cells in the center forming a four-pointed star are the xylem; the thin-walled green cells between the xylem rays are the phloem. The thick-walled red endodermal cells form an interrupted ring near the margin; the thin walled green cells just inside these constitute the pericycle. (Courtesy George H. Conant, Triarch Botanical Products.)

star (Fig. 4-12). The number of rays is variable. Between the rays of xylem lie separate strands of phloem. In some roots the central cells are parenchyma-like, and then the rays, or strands, of xylem are isolated. Water absorbed from the soil by the root hairs and epidermal cells must pass through the cortex to reach the tracheary elements within the stele. Branch roots arise in the pericycle from points opposite the rays and grow through the cortex (Fig. 4-13). Thus the central xylem of the branch

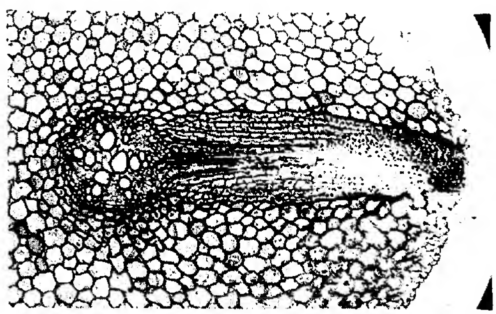


FIG. 4-13. Photomicrograph of a cross section of a root showing branch root originating from one of the xylem rays and growing through the cortex.

is connected to the xylem of the parent root and phloem is connected to phloem. In consequence there are as many vertical rows of branch roots as there are xylem rays in the parent root.

The discussion up to this point has taken into consideration only the distribution of primary tissues in the root. How the secondary tissues are added, thus bringing about secondary growth, is reserved for later consideration. At this time it is sufficient to know that secondary thickening is brought about by new cells produced by a lateral meristem called the *cambium*.

Stem Tissues. Stems vary greatly in the amount and arrangement of the vascular bundle system. A common type is characterized by vascular tissue arranged in the outline of a truncated cone. Within the cone the fundamental tissue is called the *pith* or *medulla*. The region surrounding the cone of vascular tissue is the *cortex*. Since the taper of the truncated cone is usually slight it may seem to be almost cylindrical. For this reason it is common practice to use the term "cylindrical" in describing the arrangement of the vascular tissue. In many herbaceous plants the vascular tissue is in the form of a more or less complete cylinder about a central

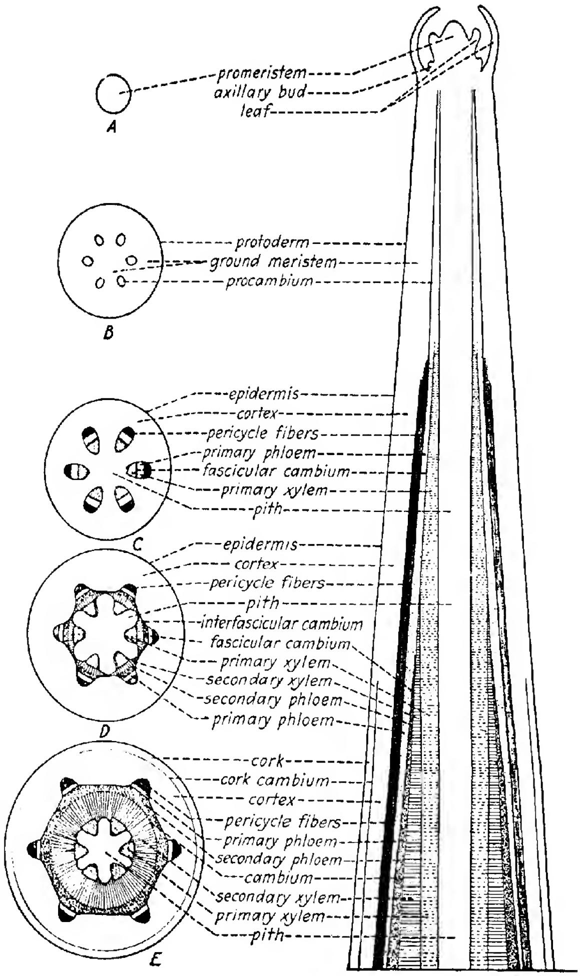
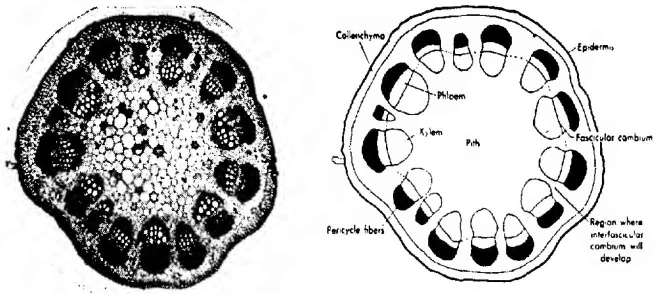


FIG. 4-14. Diagrammatic drawing showing the origin and arrangement of primary and secondary tissues in the stem of a dicotyledonous plant (modeled after a sunflower stem; lengthwise section at right, cross sections at different levels at left, *A–E*). (Drawing by F. Brown. Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)



A *B*

FIG. 4-15. *A*, photomicrograph of a cross section of a sunflower stem; *B*, diagram of same to show location of tissues.

pith and surrounded by a cortex (Fig. 4-14). In some young stems distinct bundles may be close together but separated by rays of parenchyma cells connecting the pith and the cortex. These regions are called *pith rays* or *medullary rays.*

Just outside the vascular bundles, between them and the cortex, is the *pericycle.* It is broader and less well defined than in roots. Often there are strengthening fibers, *sclerenchyma* cells, in the pericycle. In some stems these pericycle fibers are grouped on the outside of the phloem of the bundles, appearing as if they

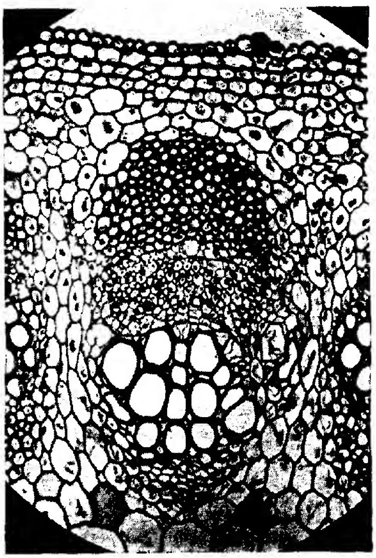


FIG. 4-16. Enlargement of one of the bundles from the preceding figure showing details of structure in the xylem, phloem, and fibers. Note also pith rays on either side of the bundle, and the strengthening collenchyma cells just within the epidermis.

were a part of the bundle (Figs. 4-15, 4-16). In other stems they are in a continuous layer around the vascular cylinder. A well-defined endodermis, such as is found in most roots, is lacking in many stems. If present it lies between the pericycle and the cortex.

In the kind of stem just described secondary growth ordinarily occurs as a result of cambial activity. This type of stem is characteristic of the great group of seed plants known as *dicotyledons.* Here belong many of our common herbaceous plants and trees with netted veined leaves. In another type of stem the bundles do not possess a cambium and are often scattered throughout the fundamental parenchyma; the limit of cortex, pericycle, and pith is indistinguishable. In many stems of this sort the central cells disintegrate, with the result that the stem becomes hollow, except at the node. This type of stem is characteristic of the group of seed plants known as *monocotyledons* (Fig. 4–17). Here belong grasses, lilies, and many plants with parallel veined leaves.

The epidermis of young stems is much like the epidermis of leaves. In general it consists of a single continuous layer of cells. Stomata are present

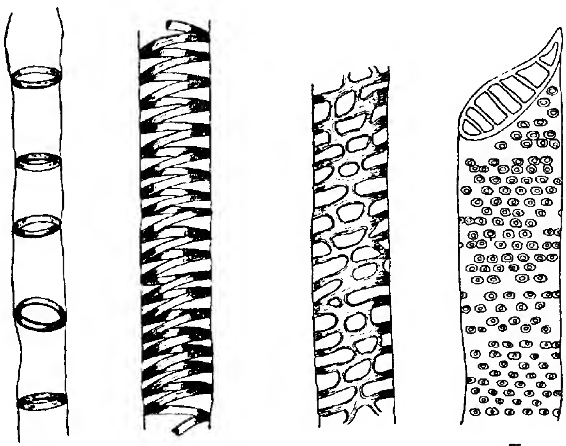


FIG. 4–18. Four types of conducting vessels. *A*, annular; *D*, spiral; *E*, scalariform; *F*, pitted with scalariform end wall. (Drawings by F. Brown. Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

but usually much less numerous than in leaves. The outermost cortical cells are often thickened at the corners or angles and are called *collenchyma.* They function as strengthening tissue in young stems. The phloem of the bundles contains sieve tubes, smaller cells accompanying them known as companion cells, ordinary parenchyma cells, and sometimes also scleren-

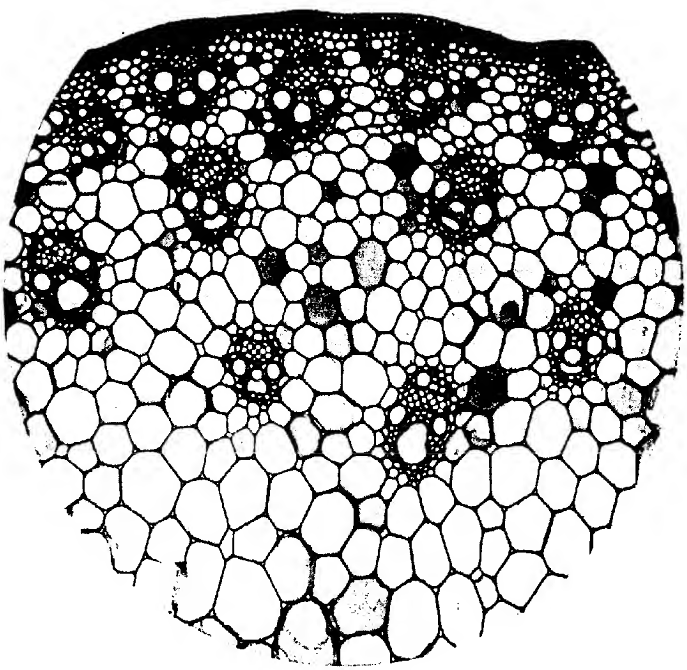


FIG. 4-17. Cross section of a monocotyledonous stem (corn) showing scattered bundles, pith, and the small cells, with thick lignified walls, which form a protective rind inside the epidermis. (Courtesy George H. Conant, Triarch Botanical Products.)

chyma fibers. The xylem is made up of tracheids, tracheae, wood fibers, and parenchyma cells. In the younger growth the vessels are usually of the annular or spiral types (Fig. 4–18). In the annular type there are thickened rings on the inside something like a barrel would be if the hoops were on the inside. These thickenings of various sorts in the walls of conducting vessels make them strong so that they will not collapse from outside pressure or internal tension. The spiral type is also common in young regions. In older regions the walls of the tracheae are frequently thickened but have thin areas or pits. Sometimes the thickenings are more or less crosswise and bar-like, giving a ladder-like appearance which has been called *scalariform*. The wood fibers are elongated and pointed, and have thick hardened walls. The walls of the cells of woody tissue consist chiefly of *lignin* which is added to the original cellulose. Lignin makes the walls firm and hard but does not interfere with the penetration and passage of water. The cells of the medullary rays and the pith are of the parenchyma type and function chiefly for food storage.

A concept of the distribution of the tissues in the stem and the character of the cells will be aided greatly by a study of the accompanying illustrations. Cross sections show the distribution best, but many cells must be seen in lengthwise view if we are to get an idea of their shapes and markings. Therefore, longitudinal sections or macerated tissues in which the cells have been separated are important for studies of the individual cells.

The Secondary Tissues

We have already referred to the familiar fact that stems grow both in length and in thickness. This may be equally true of roots although not so readily appreciated. The growth in length we call primary growth. It is brought about by cells added to the ends of stems or roots by the meristem at the stem tips and root tips. The tissues formed as these cells, which are at first all alike, differentiate into various kinds of tissues are called the *primary tissues.*

After growth in length has ceased, secondary growth begins by the addition of *secondary tissues* to the primary tissues. The secondary tissues are formed by a lateral meristem to which is given the name *cambium.*

The Cambium. A layer of cells lying between the xylem and the phloem called the *cambium* does not differentiate but remains meristematic. If the bundles are separate, the cambium of a bundle is called the *fascicular cambium.* Between such bundles, and continuous with the fascicular cambium of the adjoining bundles, there develops in the ray tissue what is aptly called the *interfascicular cambium* (Fig. 4–19). The fascicular

and the interfascicular cambium become joined to form a complete *cambium cylinder*. If we were to be exact, we could not use the term cylinder because stems and roots are not really cylindrical but taper upwards and downwards respectively. In cross sections the cambium appears as a circle. In woody stems the cambium region is easily recognized between the wood and the bark. The cambium cylinder (we shall continue to use that expression) consists of a single layer of cells, but in a cross

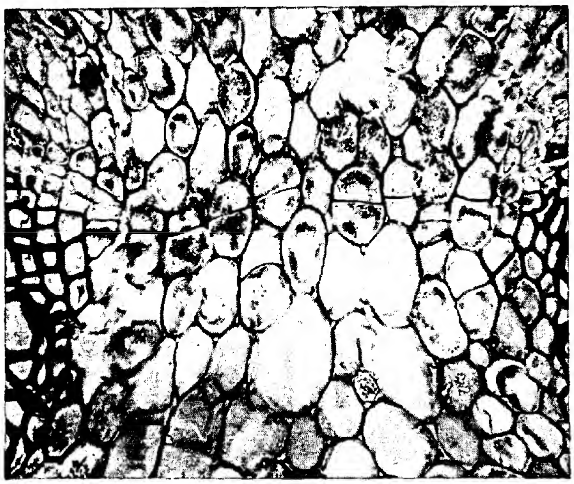


FIG. 4-19. Photomicrograph showing how the interfascicular cambium arises by tangential divisions of pith ray cells between the bundles.

section it may appear to be several layers in thickness because cell division goes on faster than differentiation. The cambium cells divide both tangentially and radially. The tangential divisions make possible the additional layers of cells. The radial divisions make possible additional cells in the cylinder, so that the added layers can be constantly larger, thus enabling them to reach around an axis which is constantly increasing in circumference.

The cambium cylinder develops two layers by tangential divisions (Fig. 4-20). If the inner layer enlarges and differentiates, additional xylem is formed. The outer layer remains as cambium and divides again. A repetition of xylem differentiation results in the formation of more xylem inside the cambium. But it is possible for the outer layer of divided cambium to mature into phloem. In such a case the inner layer remains

cambium. In this way cambium activity builds up a new layer of xylem over the preceding xylem and a new layer of phloem inside the preceding phloem. As a rule the differentiation is more often into xylem than into phloem so that the zone of secondary xylem is thicker than the zone of secondary phloem.

The Cork Cambium. Up to this point we have considered only the formation of secondary tissues in the vascular cylinder. Even if we cannot

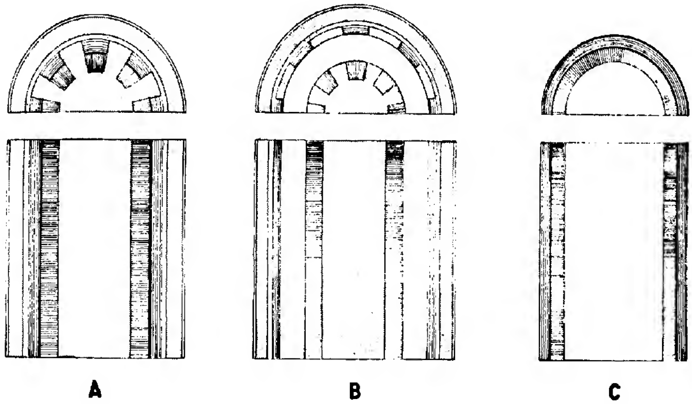


FIG. 4–20. Diagrams showing primary and secondary growth, *above* transverse sections, *below* longitudinal sections. *A*, the first-formed stem as it is built up by primary growth. *B*, secondary growth formed by cambial activity pushes apart the primary xylem and the primary phloem. In this diagram the space which the secondary growth occupies is vacant. *C*, the masses of secondary xylem and secondary phloem which really occupy the vacant space in *B*.

present the details fully, the fact will be recognized that there must be a secondary increase in the tegumentary system and in the cortical region to provide for the increasing diameter of the vascular cylinder. In woody plants the epidermis is replaced by a layer of brownish cork tissue derived from a lateral meristem called the *cork cambium* which arises beneath the epidermis. The cork cambium develops new layers of cork cells inside of the older cork layers, and may develop new cells (*phelloderm*) outside of the deeper-lying cortical cells. Thus is provided a protective coat which is capable of expanding so as to cover a stem or root that is increasing in diameter. The cork is waterproofed by the formation of *suberin* in the walls of the cells. As the epidermis is replaced by the cork, the stomata are replaced by *lenticels.* The cork functions in a manner similar to the epidermis by reducing evaporation of water from the inner tissues without preventing

the passage of gases. In a sense we may say that the lenticels are the successors of the stomata. A lenticel usually develops under a stoma and consists of a mass of loosely arranged cells with many air spaces through which gases diffuse readily. Lenticels are many-celled structures and often protrude above the surface of the bark so that they can be seen by the unaided eye. They are frequently conspicuous on young stems and their appearance and arrangement may be characteristic for a species.

The Vascular System. As the vascular cylinder develops from the cambial activity there are formed in the xylem and phloem not only the elements for upward and downward conduction, but sheets of cells which run crosswise in a radial direction. The height of the radial structures may vary from few to many cells. They are thin ribbon-like formations and there are many of them. In the xylem they are designated as *wood* or *xylem* rays and in the phloem as *phloem* rays.

The elements of the secondary xylem are provided either with transverse, slit-like, scalariform pits or with circular or oval pits. Wood fibers and wood parenchyma cells are also present. The walls of the fibers are much thickened and lignified. Sieve tubes and their smaller companion cells, fibers, and parenchyma cells are the elements of the secondary phloem. Ordinarily the secondary phloem is much like the primary phloem.

A study of cross-section diagrams is most helpful in gaining an idea of the arrangement of the different regions and the distribution of the various tissues.

When woody stems are cut either lengthwise or crosswise there are evident streaks which make them appear as if composed of layers. Concentric rings may be apparent in the end of a log, especially if it is cut smoothly and evenly. They are often so sharply defined as to be visible to the unaided eye. Doubtless many people call them annual rings without any clear conception of what the term means or without a real understanding of why they exist.

These rings represent different layers of growth. Since each layer is the growth of one year they may very properly be called *annual layers.* In cross sections these annual increments appear as rings (Fig. 4-21). By counting the number of rings in a cross section it is possible to tell the age of a stem, or of a tree if the section is taken through the trunk close to the ground. Under unusual conditions the number of rings may exceed the number of years. Destruction of leaves by insects or fire may stimulate midsummer growth so that there is a second formation of spring wood. In tropical regions where there is no climatic variation the periodicity of cambial activity is lacking in some plants and annual rings are not formed.

An interruption of growth, which might occur during a dry season, would bring about the formation of annual rings even in tropical plants.

But why does a demarcation appear so plainly between the growths of the different years? It is due to the fact that the structure of the cells in the early spring is different from that of the cells produced later. The terms *spring wood* and *summer wood* are commonly used for the growths

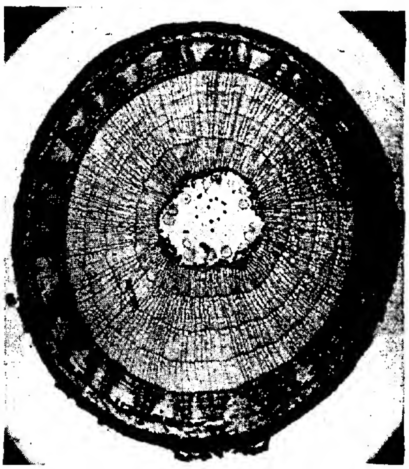


FIG. 4–21. Photomicrograph of a cross section of a four-year-old stem of *Tilia* (basswood) showing annual layers in the xylem (wood), and less evident, but still apparent, rings in the dark phloem surrounding the lighter xylem.

produced in these seasons. In the spring there is a large-celled soft growth which turns into a hard reddish growth in late season. At the end of a season's growth the cambium rests until the following spring. In tropical woods it may not be easy to tell one ring from the next, but in temperate climates the demarcation between the summer wood of one year and the spring wood of the next year is distinct.

The thickness of an annual increment varies with different seasons and in different plants (Fig. 4–22). Some trees grow rapidly, producing wide increments, whereas others grow slowly, producing relatively narrow rings. Slower growth usually produces harder wood. Even though large tubes may be formed in the spring, growth may be sufficient for the small heavy-walled cells of the summer growth to produce a solid hard wood. The appearance of the wood may be affected greatly by the character of the

wood rays. They form radial structures of varying prominence. In a lengthwise section they may show up conspicuously if the section parallels the radius fairly closely. Quarter sawed oak owes its effect to these wood rays.

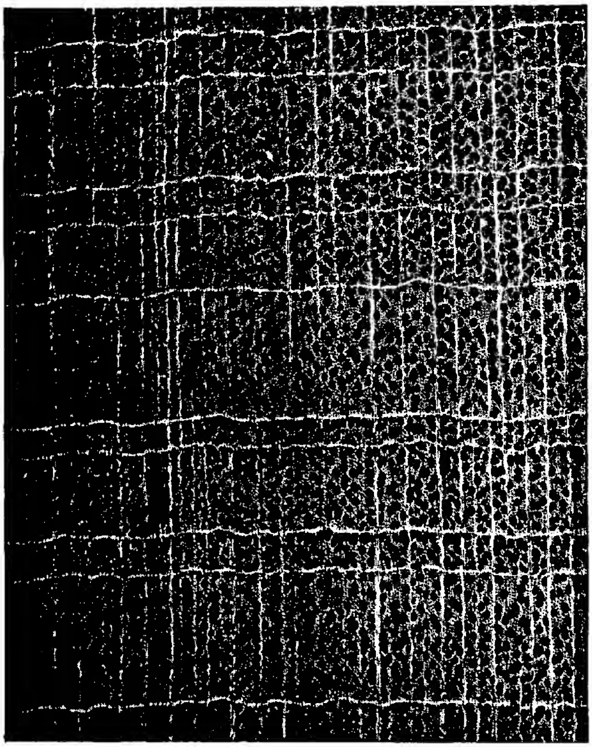


Fig. 4–22. Photomicrograph of wood of tulip poplar showing annual increments varying in thickness in different seasons. The large vessels are more or less evenly distributed throughout the growth of each season. (Photograph by D. A. Kribs.)

The so-called soft woods do not have a band of large tubes in the spring wood, but the cells are larger there and annual rings are evident. In the wood of these trees there are often present large intercellular canals which are resin ducts (Fig. 4–23). Many of the hard wood trees have such large conspicuous vessels in the spring wood that they appear as pores and the term *ring-porous* is sometimes used to describe such woods (Fig. 4–24).

Since the growth of trees is influenced by the conditions of the environment their rings record the effects of favorable and unfavorable years. Studies of old trees, such as the redwoods, have revealed the records of drought, rainfall, and sunspots for hundreds of years. These tree-ring

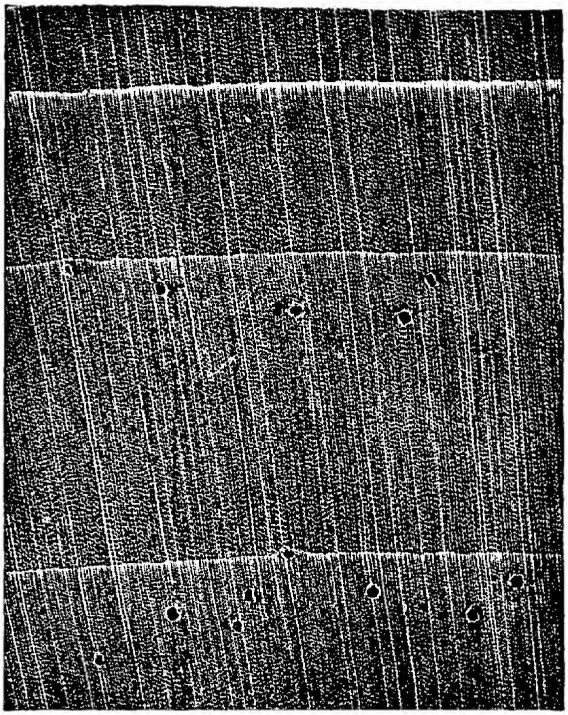


FIG. 4–23. Photomicrograph of wood of white pine. The cells are of rather even size except those at the outer part (upper in picture) of each annual increment. The large, dark, scattered openings are resin ducts. (Photograph by D. A. Kribs.)

chronologies, as they are called, make possible a historical study of climatic cycles. Such studies may lead to an estimation or prediction of future conditions. Tree-ring studies of pines have developed another important possibility—that of dating the age of beams in ancient ruins of cliff dwellings and other events in the history of ancient peoples. The rings tell a story of the time of building as to both the number of years involved and the order of building, facts of interest to anthropologists and archeologists.

For the relation of tree rings to climatic cycles and dating problems we are indebted to the work of A. E. Douglass.[1]

The secondary xylem makes up the greater part of the vascular system in many plants. In woody plants it constitutes the bulk of the entire plant

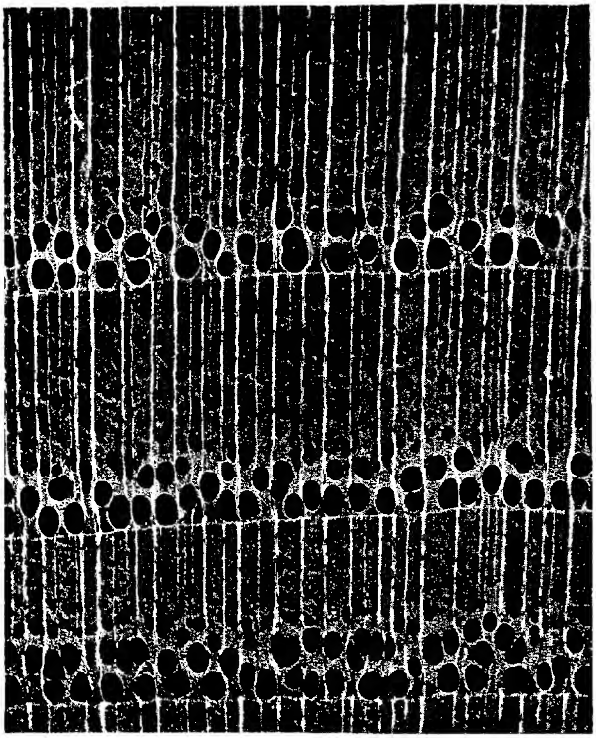


FIG. 4-24. Photomicrograph of wood of slippery elm. Large vessels appear in the spring growth forming what is known as ring-porous wood. (Photograph by D. A. Kribs.)

body. The wood and lumber of commerce is the secondary xylem of tree trunks. In the modern world wood is finding an ever-increasing use. Wood can be made into substitutes for wool and cotton. From it sugar and alcohol can be obtained. By impregnation and the application of heat and

[1] *Publications* of the Carnegie Institution of Washington, 1914, 1919, 1928, 1936; papers in the *Scientific Monthly*, 1925; *Nature Magazine*, 1928; and University of Arizona *Bulletin*, 1937.

pressure wood products can be made which have strength and durability approaching that of steel. Wood products are made into plastics which may be "lighter than aluminum, as transparent as glass, as soft as rubber, as flexible as lead." Wood is certain to be a substantial factor in the raw material market of the future.

In woody stems there are two well-defined regions, the *bark* and the *wood,* separated by the cambium. The bark in older stems may be differentiated into the *inner* and the *outer* bark. The inner bark is made up of active secondary phloem. The outer bark consists of dead phloem, the remains of the cortex, and layers of cork. On the stems of most shrubs and trees the outer bark cracks and may slough off.

Many roots increase in diameter in a manner which is similar to that in stems. Secondary growth results from the development of a cambium between the xylem and phloem. Woody roots of trees or shrubs show annual increments and have about the same structure and appearance as a stem of the same age.

We may summarize by saying that woody stems and roots increase in diameter by activity of two cambiums, one in the vascular cylinder and one in the bark. The cambium of the vascular cylinder might well be known as the vascular cambium but it is usually designated as *the cambium.* It adds new layers to the *exterior* of the wood and to the *interior* of the bark. The cambium of the bark is the *cork cambium.* It develops layers of cork within the epidermis and keeps on adding new layers within the old cork.

GROWTH

A seed germinates and the little plant (embryo) which was within the seed develops into a seedling (Fig. 4–25). The seedling increases in size, new branches and leaves develop, and later flowers appear. The enlargement of the trunks of trees and the extension of their branches, although gradual, are nevertheless familiar phenomena. These developments and increases in size are manifestations of growth. Growth usually results in an increase in weight, a change of form, and an increase in the size and number of parts. Spring is the season when growth is most evident; new seedlings appear on every hand, leaves burst from the dormant buds, and new branches develop. Most plants grow by repetition of similar parts, new leaves, new stems, new roots, and new flowers forming in succession. "The nature of growth has been as eagerly sought as has been the explanation of life itself."

The Factors Influencing Growth

Since growth is the result of several physiological processes it is affected by several factors, of which some are internal and others external.

Among the internal factors which affect growth are heredity, growth regulators, nutritional balance, and the interrelation of plant parts. The form, and to a certain extent the rate of growth, are determined by a group of factors inherited from the preceding generation. These inherited factors constitute heredity. An acorn is the fruit of an oak and in turn the acorn develops into an oak. The

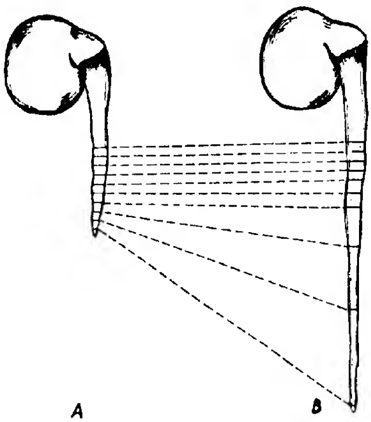


FIG. 4-25. Growing region of a root of a pea seedling. *A*, root marked into 1 mm. spaces. *B*, the same root 24 hours later. (Drawing by F. Brown. Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

embryo in the acorn inherits the capacity to become an oak and no conditions can cause it to develop into any other kind of tree. Heredity is a most important factor in growth and development.

For some years it has been known that there are glandular secretions in animal bodies which influence basic life processes. It is known that similar substances are present in plant bodies. Two terms have been used for these compounds, ***hormones*** and ***auxins***. They are also called growth regulators or growth substances because of the influence that they exert on growth. In discussing hormones emphasis is frequently placed on the fact that they may be produced in one part of a plant and may control or influence a process in another part. The term auxin is generally used for those substances considered to be growth regulators. It should be emphasized "that they are used to condition the growth of the organism rather than to build its structure, as mineral salts, sugars, and proteins are used." In addition to the growth-stimulating substances naturally occurring in plants there are some substances, which are not plant products, that have more or less similar effects. Some of the synthetic hormones are used in practical ways. Indoleacetic and indolebutyric acids accelerate the growth of roots on cut-

tings (see Fig. 8–5). Naphthalene acetic acid or naphthalene acetamide is used for spraying fruit trees to delay the falling of fruit. The spray solution delays the organization in the fruit stem of a separation zone (abscission layer), the weak place where the fruit separates from the tree. Leaf fall, which is also effected by an abscission layer, is also retarded by the spray but for a shorter time than in the case of the fruit.

Vitamins are a group of organic substances known to have important effects on the growth and good health of animals. It is not certain how significant they may be in plant life and development. Since green plants synthesize them within their bodies, experimentation is difficult. Scientists are now discovering some of their functions in plants. It has been definitely proved that certain vitamins are growth substances for fungi and bacteria and also for higher plants. Vitamin B_1 is essential for root development. Vitamins are not classed as foods. They have been so regarded because animals get their supply of vitamins with their food.

The relative proportions of carbohydrates, fats, and proteins, or the nutritional balance as it is called, may also have much to do with growth. Abundance of carbohydrates may favor reproductive activity, whereas an excess of nitrogen may promote a vegetative but unfruitful development. The interrelation of plant parts is known to be important in the development of a plant. This is demonstrated by the removal of a part. If the end of a branch is removed some of the lower buds, which otherwise would have remained dormant, are stimulated into growth. It is a well-known fact that the shape of a fruit tree and also its tendency to bear fruit can be changed by pruning.

Among the best-known external factors affecting growth are light, temperature, and moisture, but there are many others. The supply of oxygen, mineral salts, and carbon dioxide is important; gravity, electricity, wind, insects, and diseases also may have a bearing on the form and rate of development.

Light is necessary for the formation of chlorophyll and for photosynthesis, and if insufficient for these processes growth is retarded or is not normal. Plants grown in the dark are yellow and spindly, and have undeveloped leaves.

Reference has been made previously (Chapter 1) to the effect of length of day on the growth of plants into a vegetative condition or a reproductive condition. Some plants, such as radish, lettuce, or hibiscus, bloom normally in midsummer and are called *long-day* plants. Others, called *short-day* plants, bloom in spring or autumn when the days are comparatively short. Most of the spring flowers and the autumn-flowering chrysanthemums,

asters, and ragweeds are examples of short-day plants. Some plants such as chickweeds, dandelions, tomatoes, and buckwheat respond to different lengths of day and bloom any time during the growing season. Chrysanthemums can be brought into bloom by being shaded in such a way as artificially to produce the effect of shorter days. Experiments have shown that some plants can be hastened into bloom in a shorter number of days than usual by lengthening the daily light period with artificial light. Some plants show obvious ill effects and even changes in form if subjected artificially to wide changes in the length of day. The influence of the length of the normal daylight period is of real importance in governing the time of planting of certain crops. It also affects the growing of greenhouse crops during the winter. In his recent book, *Plant Growth,* Yocum says the reason for length-of-day phenomena is not understood. "Much work," he writes, "has been done on the problem, studying such fields as nitrogen assimilation, temperature, stored food, and growth hormones, but at present the problem remains unsolved."

Temperature is a very important factor affecting the rate of growth. The range of temperature varies within the minimum (somewhat above freezing) below which no growth occurs, and the maximum (usually about 25°C.) above which no growth takes place. Between these is an optimum (around 30°C.) which permits the highest rate of growth. A rise in temperature from the minimum to the optimum increases growth. The range of temperature varies with different kinds of plants. Corn, for example, grows best on hot nights, whereas most ferns thrive under cool conditions. Even in the same plant the optimum temperature for root and shoot may be different. In starting bulbs, the bulbs are kept in a cool environment for root growth and moved to higher temperatures for later growth and flowering.

Water is so important in the growth of plants that much of the following chapter is devoted to its consideration. The relations of soils and of diseases and pests to plant growth are topics also discussed in succeeding chapters.

CHAPTER 5

THE SUPPLY OF RAW MATERIALS

(Absorption, Conduction)

The raw materials for which plants are dependent upon their environment are carbon dioxide, water, and certain minerals. Some of the facts about these essentials and their uses in the plant have been discussed in preceding chapters. Other facts about their mode of supply, their entrance, and their movements within the plants are significant and must be considered. These raw materials are constantly in movement or circulation in the environment—carbon dioxide in the air, water and dissolved substances in the soil. The plants remain fixed in one place; the widely distributed but not always abundant raw materials come to them. Although bound in the living plant bodies for a time, these materials are ultimately released and again made available to plants.

WATER RELATIONS

The bodies of both plants and animals contain a large amount of water. It is a safe general estimate that more than three-fourths of the total weight of either plant or animal bodies is due to water. There is considerable variation in different plants or plant parts. Woody parts may not contain more than 50 per cent water. Juicy fruits may have as much as 95 per cent, whereas dry seeds may have as little as 10 per cent. As a rule the young growing parts of a plant contain more water than the older parts.

The Uses of Water

There are several ways in which water functions in plant bodies, some of a physical nature and some of a chemical nature. Under ordinary conditions living cells maintain a certain internal pressure which causes a stretching of the plasma membrane (*cytoplasm* next to the wall) and, to some extent, of the wall. A cell in this condition of being distended by internal pressure is said to be *turgid*. It is the absorption of water which

maintains this essential condition of rigidity of the cells and tissues and prevents wilting. We have referred to the dryness of seeds—they may be so dry that they apparently are dead. One of the essential factors leading to a reawakening of seeds is water. Without water there is no growth. The stored food can be converted into soluble form only in the presence of water. Water is the medium in which the cellular reactions take place. It is water which serves as the solvent of the sugars and other substances. The required mineral salts of the soil can enter only when dissolved in water. Thus water is necessary both for the entrance of materials and for their movement from one part of the plant to another. Previously we learned that water and carbon dioxide are the essential raw materials in the formation of foods. They provide the elements hydrogen and oxygen which go into the making of carbohydrates. Water is therefore essential in the first step of the synthesis of organic matter from inorganic materials.

From these facts it can be seen how water is indispensable for permeating and distending the cells and how it serves for the formation, solution, and transportation of the various compounds in nutrition. On the other hand, while land plants retain and use a large amount of the water which they take up through their roots, they lose a still larger quantity through their aerial parts. The loss is chiefly through the leaves in the form of vapor as a result of evaporation.

Since water plays such an important role in the constitution and life of a plant it is evident that we must give attention to the processes involved in the entrance of water, its movement within the plant body, and its escape therefrom. Likewise attention must be given to the movement of materials dissolved in the water.

Absorption of Water

Plants which grow in the water do not require special absorbing structures. Land plants obtain their water from the soil and we find that they are provided with the means for absorbing soil water. The lower land plants, such as mosses and liverworts, have structures known as rhizoids. These plants usually grow in moist places and the rhizoids are chains of elongate cells which penetrate the soil to some extent but not to any considerable depth. The higher land plants absorb water through the roots. Root systems may be much branched and extensive. In our discussion of roots we referred to the fact that water is absorbed by the young and delicate terminal parts of the roots. It will be recalled that the absorbing surface of these young parts is greatly increased by a multitude of radiating *root hairs* just a little way above the root tip. These hairs are tubular

extensions of the epidermal cells and are the active water-absorbing parts of the root.

Our study of roots, stems, and leaves has revealed the presence of vascular bundles which are continuous from the region of the root hairs through the extent of the root and upward through the shoot and into the veins of the leaves. Water from the soil enters the root hairs, passes through the cortical cells of the root until it reaches the xylem ducts of the vascular bundles, and is conducted upward through them. Living cells in the stem or in the leaves in turn take water from the ducts. These living cells appropriate some of the water to their own uses. A considerable portion, however, evaporates from their walls into the intercellular spaces and eventually escapes to the atmosphere through the lenticels and stomata. Such is a brief statement of the water relations—water enters the roots, passes through the stem, some of it is assimilated, some of it is held in the living cells, and much of it escapes as vapor from the leaves. There is a current of water through the body of the plant from root hairs to leaves. These facts can be easily learned, but our troubles arise when we consider the physical forces which are involved and all the reactions which must take place. After we have done our best, there will remain some problems for which no wholly satisfactory solutions have been found. Nevertheless, we are justified in making the effort to get the facts before us and to interpret them as fully as possible.

Osmosis and the Entrance of Water

Root hairs present to soil spaces a wall lined with living protoplasm. The part of the protoplasm which lies next to the wall is the *plasma membrane*. The interior of the hair is a large vacuole filled with cell sap. This sap is a solution whose solvent is water which has been absorbed from the soil. The water has passed through the wall and through the living plasma membrane of the root hair. It is at once obvious that water cannot *flow* through the wall and through the membrane, but it does pass through in some manner. It does not pass through by mass movement but by molecular movement. Not only does water pass from the outside into the vacuole but it does so in such quantity that a water (hydrostatic) pressure is developed within the cell. The protoplasm is pressed with real force against the wall. Physiologists say that such a cell is *turgid* and they speak of the pressure of the cell content against the wall as *turgor pressure*. The movement of the water into the root hair is a physical process known as *osmosis*.

We may proceed by describing some simple experiments. If we tie a

membrane (parchment or pig's bladder), which is permeable to water, over the end of a thistle tube filled with a sugar solution (syrup) and then support the tube in a beaker of water, we have what may be called an *osmotic system* (Fig. 5-1). Shortly the sugar solution rises in the tube. If the membrane is more permeable to water than to sugar there will be a continued rise in the tube. If the sugar molecules pass through the membrane readily the rise soon subsides. Again, if instead of pure water in the beaker we use a sugar solution but with a lesser amount of sugar than is in the solution in the thistle tube, there will be a rise in the tube as before, but it will develop more slowly. We might tie a membrane into a small bag filled with a solution and place the bag in a dish of water. Solutes other than sugar may be used. If the bag were limp when placed in the water we would find that water soon enters it, making it swell

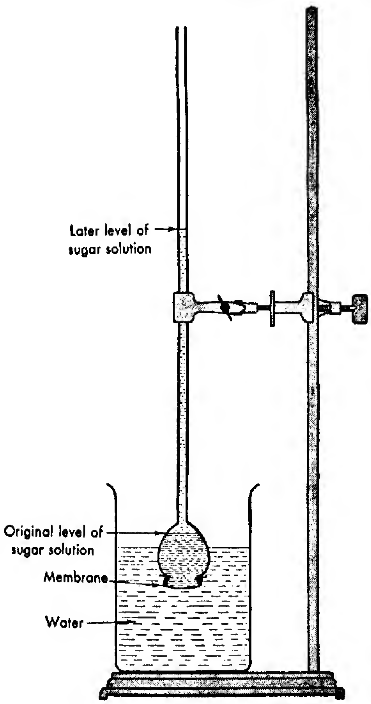


FIG. 5-1. An osmotic system; further particulars are given in the text.

from a definite internal pressure. In this bag we might have conditions similar to those in living plant cells. Whether this is the situation will depend upon the nature of the membrane used for the bag. Water passes readily through some membranes, but certain solutes do not. Membranes which differ in their permeability to different substances are said to be *selectively* or *differentially permeable.* The protoplasmic membrane of a living cell is an example of this type of membrane. Inorganic substances pass through it more readily than organic substances.

The facts are these: When water is separated from a solution (water plus a dissolved substance such as sugar) by a *selectively permeable membrane*

there is an excess movement of the water through the membrane into the solution. If two solutions of different concentrations are thus separated there is an increase in the volume of the solution of higher concentration at the expense of the solution of lower concentration. It is necessary that we analyze the preceding statement carefully lest we fall into an erroneous concept. We would doubtless all have a tendency to call a solution with *less* sugar the one of *low* concentration and a solution with *more* sugar the one of *high* concentration, and we would be correct if we are referring to the dissolved substance, sugar, as determining the *low* or the *high* of concentration. But if we are considering the water, the situation is reversed, for its concentration is *lower* in the solution containing *more* sugar and *higher* in the solution containing *less* sugar and still higher where there is no sugar, i.e., in pure water. The physical chemist tells us that there is a general law that gases and liquids and dissolved substances move from places where they are more concentrated to places where they are less concentrated, from where they are abundant to where they are scarce. In osmosis water behaves in accordance with this law of diffusion. A fuller account of diffusion is presented later in this chapter in the discussion of the entrance and movement of mineral salts.

We may try another experiment which will throw additional light on our problem. We have said that water enters the root hair through the protoplasmic membrane because the concentration of the water is less within the cell than it is in the soil water—the water moves to the place of its lesser concentration. We have reached the conclusion that the water is less concentrated within the cell because more dissolved substances are there. If now we reverse the situation and place around the root cells a solution which has more dissolved substances than the cell sap contains, water should leave the cell. We find this to be true. So much water may leave the vacuole that the protoplasmic membrane is no longer pressed against the cell wall, but withdraws from it toward the center of the cell. This contraction of the protoplasm in an active cell is known as *plasmolysis* (Fig. 5-2). If continued long enough the end result will be a rounded mass of protoplasm in the center of the cell.

It will be helpful to keep in mind that osmosis involves molecular movements. Everyone knows that water evaporates. The fact is that some of the water molecules on the exposed water surface leave the water and pass off into the air. There is no chemical change. The water molecules may be associated to form liquid or to form vapor. The tendency of the water molecules to escape into the air is known as vapor pressure. There are differences in the vapor pressures between pure water and solutions and be-

tween solutions containing different amounts of dissolved substances. Evaporation goes on faster from the surface of pure water per unit area than it does from the surface of a watery solution. The theory is that more water molecules are exposed per given area on the water surface than are exposed on the solution surface. That explains their more rapid escape. Now let us apply this to the separation of water and a solution by a membrane. Similarly there are more water molecules against the membrane

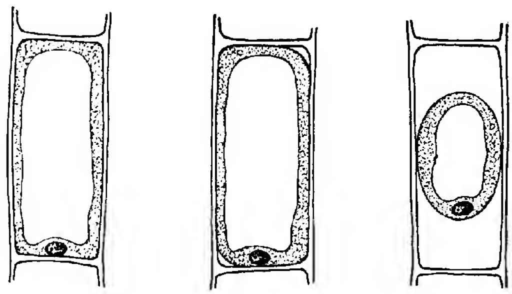


FIG. 5-2. Turgor pressure and plasmolysis in corn root cells. *A*, in water: The protoplasm is pressed with force against the wall and the cell is turgid; *B*, in 2.3 per cent potassium nitrate, showing slight plasmolysis; *C*, in 5 per cent potassium nitrate, showing a high degree of plasmolysis. (After Pfeffer.)

per given area on the water side than on the solution side (Fig. 5-3). Thus we see that the water molecules would enter the membrane at a more rapid rate from the water side than from the solution side. In turn the water molecules would leave the membrane at a more rapid rate on the solution side. The net result would be an excess movement from the water into the solution. The same reasoning applies to the separation of two solutions of unequal concentration. There are relatively more water molecules on the side of the weaker solution; hence the excess movement of the water is from the weaker solution to the stronger solution. The water is diffusing from the region of its higher concentration to one of its lower concentration. Of course the water molecules are moving in both directions but at a greater rate in one direction than the other; the end result is accumulation in the direction in which the rate is more rapid.

Restatement of Osmosis

Osmosis is a difference in the rate of movement of solvent molecules from opposite sides of a selectively permeable membrane separating two

solutions of different concentrations of the solvent. In plants the selectively permeable membrane is the peripheral layer of protoplasm (plasma membrane) surrounding living cells, and the solvent is water. Osmosis cannot be defined simply as "diffusion through a membrane." Osmosis

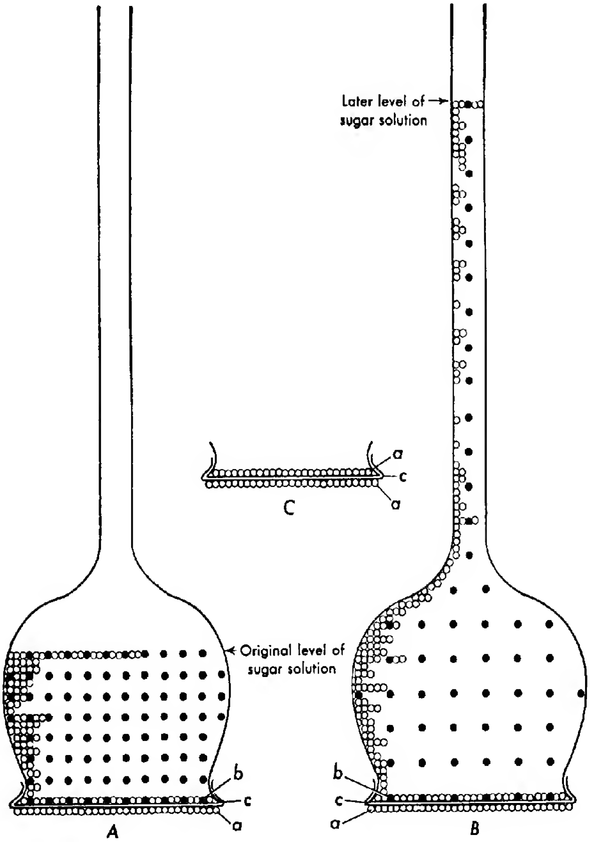


Fig. 5-3. Diagrams to illustrate osmosis. *A*, water molecules (*a*) on the outside of membrane (*c*) and water molecules (*a*) and sugar molecules (*b*) on inside of membrane. There are fewer water molecules in contact with the membrane on the inside; hence the water passes in more rapidly than it passes out, and the level of the solution rises as in *B*. Note that the sugar molecules become more widely separated. If equal numbers of water molecules are in contact on both sides of the membrane as in *C*, the movement of water molecules is the same in each direction and the level of the water will remain unchanged.

is a special case of diffusion which is a dispersal of material by molecular movement. In the dispersion of materials by diffusion everything moves from a region of abundance to a region of scarcity, so far as other features of the environment permit. When pure water is on both sides of a selectively permeable membrane the water molecules are diffusing through the membrane. In such a case the rate of diffusion from the opposite sides is the same; hence there is no osmosis. The phenomenon of osmosis appears only when there is an excess diffusion of water in one direction. The excess diffusion takes place when there is a difference in the concentration of the water molecules on the two sides of the membrane—or we might say when there is a difference of diffusion pressures on the two sides of the membrane. Water molecules are more abundant when there are fewer molecules of a dissolved substance (solute) present; hence the excess movement is always toward the solution having the higher concentration of the solute.

Living plant cells when mature are enclosed structures. The wall and peripheral protoplasm surround a large central vacuole filled with a solution of organic and inorganic solutes. When water, or a solution of lower concentration of solutes, is outside such a cell there is a movement of water into the cell. The volume of the solution in the vacuole is increased and the protoplasm is forced against the wall by the expanding vacuole. This pressure, which is the *result* of osmosis, is called *turgor pressure*. This should not be confused with *osmotic* pressure which is the *cause* of osmosis. Since osmosis is caused by the presence of solutes, and since the extent of osmosis is dependent upon the concentration of the solutes, the term *osmotic pressure* is used to refer to the maximum capacity of a solution to produce osmosis under perfect conditions. Osmotic pressure is a potential rating; *turgor pressure* is the actual pressure produced. If a solution outside a cell contains more solutes than the cell sap, water will move out of the cell faster than it moves in, and the protoplasm shrinks. In this condition the cell is said to be *plasmolyzed*. In a plasmolyzed cell the potential pressure of the cell sap is high, but there is no actual pressure; osmotic pressure exists but is not being expressed as turgor pressure under such a condition.

Osmosis is a process of outstanding biological significance. It is a factor in the entrance and distribution of water. The development of turgor pressure within cells is a feature of great physiological importance. The rigidity of the soft and succulent parts of plants is dependent upon turgor. Increase in the size of cells in growth is dependent upon the entrance of water by osmosis. Certain movements of plant parts are brought about by

changes in turgor. Osmosis and turgidity of cells are the basis of many processes which are fundamental to the development and behavior of the living plant.

Imbibition

It is believed that the prominent place given to osmosis in the entrance of water into the plant body is justified. Our account would not be complete, however, if we did not give consideration to *imbibition*, which plays a part in the absorption of water by living cells. A dry piece of gelatin absorbs water and shows the effect of the absorption by an increase in volume. Dry wood absorbs water—it will even absorb water from the vapor of the air—and there is frequently a noticeable swelling as is evidenced by the sticking of doors and windows in wet weather. The absorption of water by such materials as gelatin or the lignified cell walls in wood, with the accompanying swelling, is called *imbibition*. Dry protoplasm (as in seeds) absorbs water by the process of imbibition. There may be other substances in the cell which imbibe water. The forces involved in the swelling of substances in imbibition are a manifestation of the energy of diffusion.

The outer layer of the wall of root hairs is gelatinous material which causes the hairs to adhere to particles of soil and brings them into intimate contact with soil water. This gelatinous layer, and also the inner cellulose layer, absorb water by imbibition. Since imbibition brings the water into contact with the plasma membrane, it plays a role along with osmosis in the absorption of water from the soil by the root hairs.

Conduction of Water

We have already pointed out that water entering the root hairs passes through the cells of the cortex until it reaches the vascular system. The vascular bundles are continuous and unbroken, though much branched, from roots to leaves. There can be little doubt that there is a streaming, or mass movement, of water through the tracheary elements of the xylem. It will be recalled that there are two parts of a vascular bundle, the xylem and phloem. Age-old experiments prove that the principal movement of water is in the xylem, i.e., the wood (Fig. 5-4). If we take a twig, remove a section of the bark completely (this is known as girdling), and place the twig in water the leaves will remain fresh for a considerable time. Since the phloem was removed with the bark and only the wood (xylem) remains there seems no reason for doubting that the wood is functioning for the passage of water. But the converse of this experiment can be carried out by removing the wood and leaving only the bark. The result

is that the leaves soon wilt. The phloem either is lacking in capacity for water conduction or, at least, is inadequate.

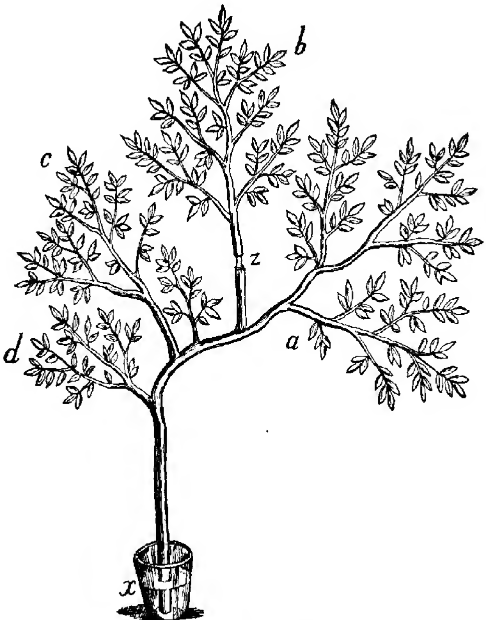


FIG. 5-4. Reproduction of an illustration by Stephen Hales in *Statical Essays: containing Vegetable Staticks; Or, an Account of some Statical Experiments on the Sap in Vegetables,* published in 1783. The following is his description of the experiments: "July 27th, I took several branches of *Currans, Vines, Cherry, Apple, Pear,* and *Plumtree,* and set the great ends of each in vessels of water *x* (Fig. 31.); but first took the bark for an inch off one of the branches, as at *z*, to try whether the leaves above *z* at *b* would continue green longer than the leaves of any of the other branches *a*, *c*, *d*,: but I could find no difference, the leaves withering all at the same time: Now, if the return of the sap was stopped at *z*, then it would be expected, that the leaves at *b* should continue green longer than those on the other branches; which did not happen, neither was there any moisture at *z*."

The determination that water is conducted by the xylem still leaves us with some interesting considerations concerning the mechanisms and forces involved.

The Transpiration Stream

Transpiration is the escape of water in the form of vapor from the aerial plant parts. A study of the quantity of water thus escaping, and of the

factors affecting the rate, comes later. At this point it is sufficient to understand that the release of vapor from leaves or green stems is a universal phenomenon in green plants. There is no counterpart of this process in animals. Perspiration is entirely different as to both meaning and method. Since quantities of water pass out through the leaves there must be a constant flow from the roots through the stems, and this has suggested the expression *transpiration stream* or *current*. It is generally agreed that the current ascends in the cavities of the xylem vessels and tracheids.

In transpiration, water evaporates from the mesophyll cells into the intercellular spaces and passes out through the stomata as vapor. The evaporation of water from the leaf cells lowers the amount of water in them. This furnishes exactly the proper basis for the passage of water from the xylem cells of the veins and veinlets to the mesophyll cells by osmosis. In other words, a deficiency of water in the mesophyll cells causes water to enter them from the xylem cells. The theory is that strong osmotic and imbibitional forces are involved and that a real pull or tension is exerted on the upper end of the water columns within the xylem elements. This is usually spoken of as the *cohesion theory* because it involves the cohesive strength of water. This theory asserts that a column of water has tensile strength and that if a pull is exerted on the top of the columns of water in the xylem tubes this pull can be transmitted along their whole length. Physicists say that an unbroken column of water possesses such tensile strength. According to this view, there is a pull causing an upward movement of water sufficient to balance the loss by transpiration.

If a shoot is cut from a vigorous plant and placed in water, no wilting takes place because water is drawn into the cut vessels. This shows that there can be an upward movement of water when no root is present. If the stem of a shoot is cut under water and inserted tightly in a glass tube filled with water, and if the lower end of the tube is inserted in mercury, there will be a rise of the mercury. With such a set-up it is possible to raise and sustain a mercury column to a height of at least 90 cm., which is more than could be accomplished by atmospheric pressure alone (76 cm.). Such an experiment demonstrates that there is a cohesion of the molecules of water and that transpiration does exert a pull in raising the column of water.

Although there have been many criticisms of the so-called cohesion theory, it constitutes the best explanation of the ascent of water in the plant body that has been offered. To a certain extent it is misleading to have so much emphasis on *cohesion*. According to the facts, *cohesion* of the water is only part of the mechanism which makes the movement possible. Even

if the water did cohere in the xylem it would remain stationary if there were not some *force* applied. The theory is that the force is a lifting or pulling force applied at the upper end. A lifting force is there. The rise of the water is made possible by cohesion, but in no sense is cohesion the cause of the movement. If we wished to place the emphasis on the forces concerned we would need to seek a different expression than cohesion theory, but to change a term is difficult even when we recognize that it is inappropriate.

It can be readily appreciated that such forces as atmospheric pressure, capillarity, and imbibition cannot account for the transpiration stream. It is inconceivable that atmospheric pressure can play a part because both ends of the xylem tubes are closed and it could not operate under such conditions. In any event water can be raised by atmospheric pressure only about 33 feet, whereas it must be raised ten or twelve times that to reach the tops of the tallest trees. Water does rise in very small tubes by capillarity, but in tubes the size of those in the xylem it would rise only a few inches, or at the most a foot or two. In capillary tubes many times smaller, the rise would be more significant. Imbibition has been offered as an explanation but is ruled out on the ground that its action is too slow to account for the movement of water at the rate it is known to ascend in trees. It seems fair to say that capillarity and imbibition are forces which may aid in maintaining the position of water but that they cannot account for its movement.

Root Pressure and Bleeding

If the stem of a vigorous plant is cut off close to the ground, water will flow after a time from the cut stem. When a glass tube is fastened firmly over the stump by means of rubber tubing the exuded water will rise gradually in the tube (Fig. 5-5). Under certain conditions it may attain a considerable height in the tube. By the use of a gauge it is possible to measure the pressure with which the water is exuded. Pressures sufficient to raise a column of water 20 or 30 feet are not uncommon; still higher pressures have been recorded. Sap may also flow from the cut or broken ends of twigs removed from trees in the spring. This exudation of sap is called "bleeding." It is well known that sap flows from maple trees when the trunks are tapped in the early spring. The century plant and certain palms are bled for sap which is used for making beverages.

The phenomenon of sap exudation from the cut stem when the entire top is removed has been called "root pressure" because it is obviously caused by forces operating in the roots. The fact that such forces are developed in the roots leads naturally to the suspicion that they may be responsible for the mass upward flow of water. If this were true the water

would be forced up by pressure from below rather than pulled up by lifting forces as previously concluded. There are numerous reasons why root pressure cannot be regarded as the cause of the ascent of sap. The most significant fact is that root pressure does not exist all the time. In fact, it is lowest when transpiration is the highest. By affixing a suitable apparatus to the trunk of a tree it has been determined experimentally that under certain conditions not only does sap not exude but that water actually flows into the tree. Such a lack of pressure could hardly exist if the sap were being forced up from below. The fact that cut branches, when placed in water, do not wilt is another indication that pressure from the roots is not necessary for sap ascent. It is also true that root pressure, even though sometimes of considerable magnitude, is still insufficient to force the sap to the tops of tall trees.

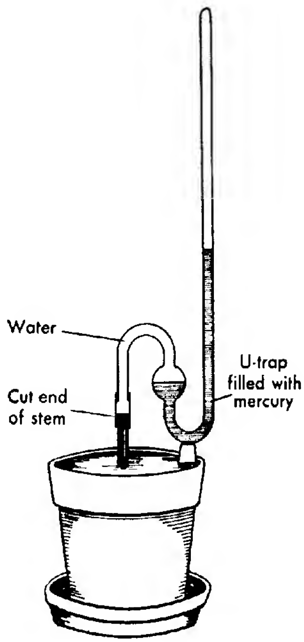


FIG. 5-5. Method of demonstrating root pressure. Water is exuded from the cut end of the stem, and the result of the pressure is evident in the rise of the mercury column.

Water Loss by Transpiration

We have called attention to the fact that a large proportion of the water which ascends through the stems of plants is lost by evaporation through the leaves. This escape of water vapor from plant parts is called *transpiration.* The chief loss is through the stomata and may be designated as *stomatal* transpiration, in contrast to the loss through the cuticle, or *cuticular* transpiration. Although cuticular transpiration may be significant, it is much less than stomatal transpiration, usually amounting to only 5 to 15 per cent of the total water-vapor loss. Theoretically, there would be no transpiration if a plant were growing in an atmosphere which was completely saturated with water vapor. Practically, such a condition does not often exist, unless it be in tropical forests, and it is therefore rare that transpiration entirely ceases. There are, however, wide variations in transpira-

tion depending upon both external and internal factors, and some attention must be given to both factors in order to gain a clear conception of what is taking place.

The really remarkable thing about transpiration is not its existence but its volume. It will be remembered that the green food-making cells within the leaves have thin walls and are filled with protoplasm and sap. If not protected by an epidermis and cuticle they would soon dry up and perish when exposed to the sun and wind. If protected so thoroughly that there could be no water loss at all, the cells would be functionless from the point of view of food synthesis and respiration. Inasmuch as there is provision for the entrance and exit of carbon dioxide and oxygen, this same provision makes possible the passage of water vapor. In other words, the same features which provide for photosynthesis and respiration provide also for transpiration. There may be some question as to whether transpiration has certain advantages or whether it is a necessary evil, but there is no question about its existence.

A large sunflower plant will transpire more than a quart of water on a warm day. A birch tree estimated to have 200,000 leaves is said to transpire 700 to 900 gallons on a hot summer day. It is calculated that an acre of such trees would give off in a growing season 3,168,000 pounds of water. Many careful studies have been carried on with potted plants in greenhouses where it is possible to make careful measurements. Ganong attempted to arrive at what he called a conventional constant, or a generalized average; his figures are 50 grams per square meter per hour (50 gm^2h) by day and 1/5 of this amount by night. Another interesting way to view the matter is to determine the amount of water given off by a plant while a certain amount of solid matter is being formed. It has been found that many plants give off 200 to 500 ounces of water for every ounce of dry solid matter produced. Some authors speak of the *water requirement* of plants. They refer to the number of units of water used for each unit of dry matter produced, and such figures can be cited: corn, 368; wheat, 513; potatoes, 636; cotton, 646; red clover, 453; ragweed, 984. After presenting these statistics it seems hardly necessary to say that the magnitude of the water requirement of plants is a matter of surprise to most people. It may be added that in general plants with lower water requirements are relatively drought-resistant.

Measurement of Transpiration

When we see wilted plants we are seeing evidence of an excessive water loss. Under ordinary conditions where there is no wilting we are unaware

of transpiration unless it is demonstrated by some means. There are several ways in which we may proceed. A fresh shoot covered by an inverted flask and held in place by a split cork, with the cut end in water, makes a good arrangement. Soon droplets of water condense on the inside of the

Fig. 5-6. Weighing method of demonstrating and measuring water loss by transpiration; further particulars given in the text.

flask. There can be but one conclusion—the air inside the flask has become saturated from the vapor transpiring from the leaves. A check may be provided by arranging in identical fashion a shoot which has had vaseline rubbed on the lower surfaces of the leaves.

There is a weighing method by which transpiration may be both demonstrated and measured (Fig. 5-6). A potted plant (fuchsia, geranium, or other greenhouse plant) is used. The pot is enclosed in an aluminum shell and the soil is covered with a sheet of rubber which is clamped to the shell and fastened closely about the stem; a bit of cocoa butter may be used here to form an airtight union. If weights are taken at intervals, a loss is noted which is properly attributed to transpiration. It is true that this experiment is subject to some errors from photosynthesis and respiration; but under

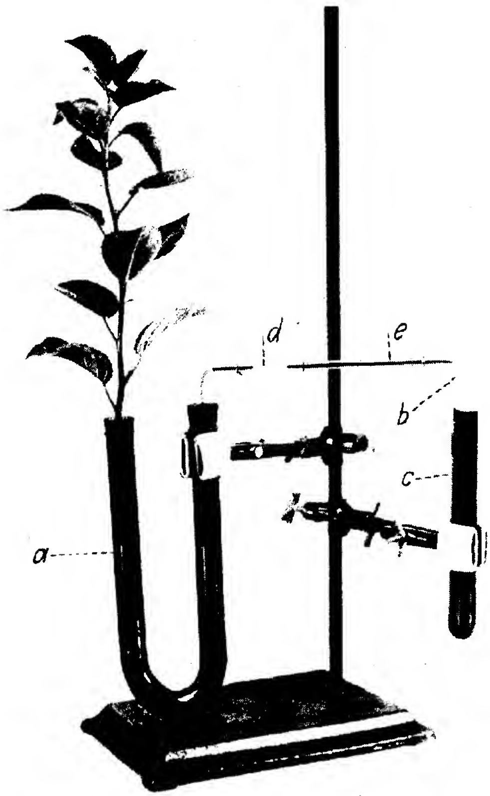


FIG. 5-7. Apparatus known as a potometer for measuring the rate of transpiration. A leafy twig is fastened through a rubber stopper into one arm of a U-tube (*a*) which is filled with colored water. A bent capillary tube (*b*) is lowered into the other arm of the U-tube until the water is forced out of the free end of the capillary tube. As water is transpired by the leafy shoot, air is drawn into the free end of the capillary tube. When a bubble of air has been drawn into the tube, the free end is lowered into a test tube (*c*) also filled with colored water. The rate of transpiration is determined by the time taken for the bubble (*d*) to move across a scale (*e*) fastened to the back of the capillary tube. To force the bubble back to the zero mark on the scale the capillary tube is pushed farther into the U-tube. The effects of light, darkness, air currents, and different temperatures on the rate of transpiration can be determined by the use of this apparatus. (Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

the usual conditions of the experiment, where the plant is kept in weak light, these are not significant. In this manner the variations in loss of weight between day and night or between warm and cold atmosphere can be compared. If the experiment is continued for several days, it may be necessary to add water to the soil; in such a case the weight readings must be adjusted accordingly. In some physiological laboratories this type of experiment is perfected so that the loss of weight is recorded on a revolving drum and a graph is obtained. If, then, on the same sheet are plotted contemporaneous graphs of humidity, temperature, and light, it is possible to see at a glance the relation of these external conditions to the physiological process of transpiration.

There are various other ways of studying and observing transpiration (Fig. 5-7). The important role played by stomata may be demonstrated by means of a color reaction. If filter paper is impregnated with cobalt chloride and dried, it is dark blue. It will change to light rose upon the absorption of water. Prepared paper strips may be applied to the upper and lower surfaces of a leaf and clamped in place by small glass plates (cover glasses). The turning of the color of the paper strips to a light rose is due to their absorption of water and hence is a proof of transpiration. If one side of the paper changes color more quickly, this is evidence of greater transpiration. It will be found that the color reaction takes place more quickly on the side of the leaf more abundantly supplied with stomata. In most ordinary plants it is the lower side. It is possible to carry out this experiment also to show that the reaction is more rapid when the stomata are open during the day than when closed during the night. It is also possible to show by this means that transpiration is more rapid in a given time from some plants than from others even though the external conditions are identical.

Factors Affecting the Rate of Transpiration

There are numerous external conditions which have a profound effect upon transpiration (Fig. 5-8). A combination of intense light, high temperature, dry air, and wind favors rapid transpiration sometimes to the point where wilting results even if there is ample soil water. The roots cannot, under such conditions, absorb water as fast as it is transpired. Light favors transpiration because it causes the stomata to open, thus permitting a free escape of the water vapor from the internal air spaces, and also because some of its energy is transformed into heat, which brings about a more rapid vaporization. Heat increases transpiration because of the physical fact that air at higher temperatures is capable of holding more vapor than air at lower temperatures. Humidity, or the amount of water vapor

in the air, is naturally an important factor in influencing the net rate at which moisture will pass from the plant to the surrounding atmosphere. Winds or air currents are significant because of their direct effect on the surrounding atmosphere. If the air immediately next to the transpiring surface is constantly changing, transpiration is increased. Barometric pressure is also a factor in determining the rate of vaporization of water. This

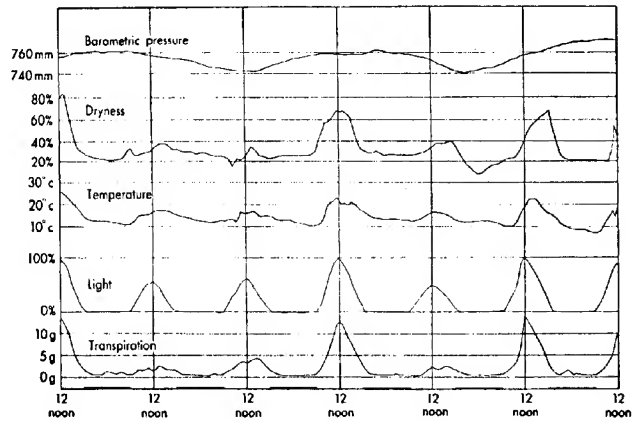


FIG. 5-8. Graphs showing correlation of transpiration with light, temperature, dryness, and barometric pressure. The graphs were plotted from data supplied by self-recording instruments, except for light which required a special method; the graph for dryness is an inverted graph of humidity. (Redrawn from *The Living Plant* by William F. Ganong with the permission of the publishers. Copyright 1913 by Henry Holt and Company.)

factor is not of importance in any given location but it does enter into the conditions between low and high altitudes. The effects of light, heat, dryness, and winds can be observed best in deserts where they prevail in a conspicuous manner. Under such conditions the ordinary broad-leaved plants do not survive; instead we find plants with reduced leaf surface and thick stems which serve as water reservoirs. Most cacti have spines which are modified leaves. Plants which possess combinations of characters that enable them to exist for a long time on a scanty supply of water are called *xerophytes* (Fig. 5-9).

This brings us to the point where we are able to conclude that the rate of transpiration is affected not only by external factors but also by structural features of the plants themselves. As already indicated, the size, shape, and arrangement of the leaves have much to do with influencing transpiration. The character of the epidermis, together with the cuticle, is impor-

tant. A double layer of epidermal cells, sunken stomata, a covering of hairs, and a thick waxy cuticle are features which reduce water loss. Xerophytic plants usually possess such characters. Sometimes transpiration is checked by a rolling or folding of the leaves. This is frequently seen in corn and other grasses.

A further word must be said about stomata and their relation to transpiration. Although the opening and closing of stomata are important factors in

FIG. 5–9. Xerophytic vegetation at a high altitude in the Andes of Venezuela. The most characteristic plant is a bushy composite (*Espeletia*). The leaves and flowers are covered with a dense woolly coating of hairs.

modifying transpiration, their actions are influenced chiefly by the conditions concerned with photosynthesis. We would expect the stomata to be open during the time that light intensity is sufficient to carry on photosynthesis, and we find that this is the case. They are commonly closed at night. Under these conditions carbon dioxide is permitted to enter freely when its entrance is advantageous to photosynthesis. It seems impossible to escape the conclusion that the regulatory features of the stomata, if we are justified in using that expression, are associated with photosynthesis and not with transpiration. Certainly the stomata are open when the external conditions are best for water escape and closed when the conditions are least favorable for water escape. Beyond a doubt their movement is influenced more by light than by moisture conditions. It has been well said that stomata do not open to promote photosynthesis and do not close to conserve water.

This raises the question whether the escape of so much water is advantageous or disadvantageous. Some workers have believed that the passage of so much water through a plant has an advantageous effect on the salt supply. On the other hand trees in tropical forests, where transpiration is less, not only show no shortage of salts but are most luxuriant in their growth. It has been suggested that the regulation of temperature is a function of transpiration. We know that evaporation does reduce temperature and it is not impossible that this feature may be a real advantage. Seifriz, in a recent book, says, "There are but two possible deductions: either the true function of excessive transpiration has not yet been learned or it is an example of the inefficiency of nature." He points out that moist tissue surfaces make possible the absorption of carbon dioxide and the elimination of oxygen—but moist surfaces also furnish the condition for transpiration. His point of view, that the maintenance of one necessary condition may force wastefulness in another respect, seems reasonable.

Although we find it difficult to answer the question whether transpiration is useful or harmful to a plant, there are certain features about the water relations and water losses of plants about which there is no doubt. We know that plants must have a sufficient amount of water. Even slight deficiencies in the water requirement of crop plants will result in reduced yields. It has been asserted that in Ohio a variation of two inches of rainfall during July may be responsible for a variation in the value of the corn crop to the extent of $13,000,000. In fruit trees not only the quantity but the quality of the fruit is affected by drought. The available water supply is one of the important factors influencing the distribution of plants over the land surfaces of the earth. Temperature is also an important factor, but its effect is due to some extent to its influence on the relative amount of water. Even resistance to freezing (hardiness) is related to the condition of the water present in the tissue. The winter killing of unprotected crops, such as wheat, is due mostly to excessive transpiration rather than to the low temperature. Trees and shrubs which shed their leaves at the beginning of a cool or dry period are for the most part perfectly protected because the water loss by transpiration has been so enormously reduced.

Guttation

Our account would not be complete without a reference to *guttation.* We have emphasized that transpiration is the giving off of water in the form of vapor. Guttation is the secretion of water in liquid form. The secretion is not pure water but contains salts and other substances. Such exudation may be seen at the tips of grass leaves and around the margins

of the leaves of such plants as cabbage and nasturtium. Doubtless much of the wetness of the grass in lawns at night is due to guttation and not to dew. A fine demonstration may be arranged with seedling wheat plants grown in a pot (Fig. 5-10). If the soil is watered and the pot covered with a bell jar and placed in a dark cool place the droplets of water will be conspicuous. This suggests that guttation is greatest when the conditions for transpiration are poorest. Guttation seems to be a process of maintaining water movement when transpiration is ineffective. The water is exuded through special epidermal structures known as *hydathodes.*

Fig. 5-10. Guttation in wheat seedlings grown in moist soil and covered with a bell jar. Drops of water appear at the tips of the leaves.

Water Storage

In connection with our consideration of water loss it is appropriate to make brief reference to some provisions for regulating the water supply through storage. Some plants actually catch and hold water in reservoirs or pockets formed by the leaves and later absorb it through hairs on the leaf surfaces. This is true of Spanish moss (*Tillandsia*) and other tropical bromeliads. They belong to a class of plants known as epiphytes, which grow upon trees without being parasites. Many epiphytic orchids absorb and hold rain water in a swollen sheath surrounding their aerial roots. In other epiphytic orchids, aroids, and ferns, humus material collects in receptacles formed by leaves or roots and holds water like a sponge until absorbed by the penetrating roots. In some plants popularly known as *succulents* there are specially developed tissues for the storage of water. The presence of mucilaginous compounds in these tissues is a factor in their water-retaining capacity. The leaves may be succulent, as in the house leek, or the stems may be the seat of storage tissues, as in the cacti. Sometimes the amount of water accumulating may be very great. It has been estimated that a specimen of giant cactus may contain as much as 30 tons of water (Fig. 5-11). The water in living storage tissues may be a part of the protoplasm, a part of the sap, or a part of the jelly-like compounds of the cell contents.

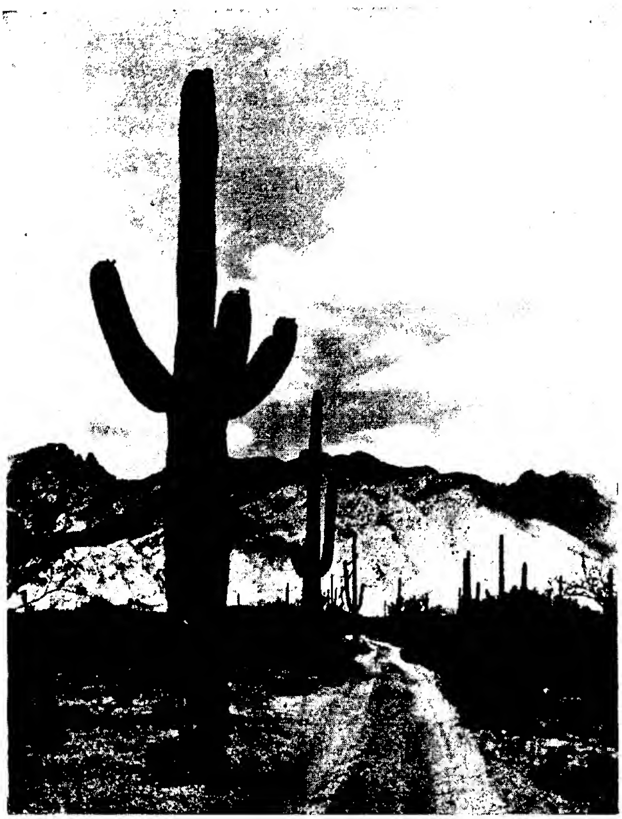


Fig. 5–11. Giant cactus (*Carnegiea gigantea*) in which great quantities of water are stored in the thick stems. (Photograph by C. J. Chamberlain, courtesy J. G. Brown.)

THE MINERAL REQUIREMENTS

We know that certain mineral salts are necessary for the life of plants. This matter has been investigated in two ways. Plants have been chemically analyzed to determine what elements they contain. A more illuminative method of research has been through water cultures. Many plants will grow if their roots are immersed in water solutions. This fact has been known by plant physiologists for a long time and they have studied the

FIG. 5-12. Water cultures of Buckwheat; *A*, without potassium; *B*, in normal nutrient solution; *C*, without iron. The glass jars (*G*) contain the nutrient solution. The plants are fixed in the median opening of the porcelain lid (*D*) by means of a halved cork which was previously soaked in paraffin. (After Pfeffer.)

salt requirements of plants in this manner. In recent years certain workers have attempted to develop the water culture method to make it practicable commercially. Its use has been confined chiefly to greenhouses or to regions with a mild outdoor climate. Some success has been attained with such crops as tomatoes and potatoes.

The term *hydroponics* has been proposed for the art of growing crops by a water culture method. No soil is used, but gravel, sand, excelsior, straw, or peat moss may be provided as an anchorage for the roots. The novelty of a soilless method of growing plants has aroused considerable popular interest. Accounts appearing in the newspapers and magazines have caused many people to seek further information about a matter which appears to have such important possibilities. It seems unlikely that many crops can be produced economically in this way. The results thus far are promising for certain crops the marketable products of which are characterized by high water content. The culture of greenhouse flowers by hydroponics may also prove successful.

By growing plants in solutions of known compositions it is possible to determine their salt requirements (Figs. 5–12, 5–13, 5–14). With such a method the effect of the absence of one element can be learned. It is possible also to reach conclusions regarding the best chemical combinations. Nitrogen, sulphur, phosphorus, potassium, calcium, and magnesium are essential. Nitrogen, sulphur, and possibly phosphorus are constituents of proteins and protoplasm; magnesium is a constituent of chlorophyll. Potassium and calcium are primarily regulators of reactions; sulphur and phosphorus may be both regulatory and nutritive.

There are certain other elements which are essential but which are required in only small amounts. They are called minor or trace elements. Iron, copper, manganese, zinc, boron, molybdenum, and possibly also chlorine, sodium, and silicon are in this class. Altogether, forty-four elements[1] have been reported to occur in plants. When plants fail to obtain their needed supply of minerals, they do not thrive and may develop characteristic disease symptoms.

[1] These elements are as follows:

Aluminum	Chromium	Lithium	Potassium	Sulphur
Arsenic	Cobalt	Magnesium	Radium	Thallium
Beryllium	Copper	Manganese	Rubidium	Thorium
Borium	Fluorine	Mercury	Scandium	Tin
Boron	Gold	Molybdenum	Selenium	Titanium
Bromine	Hydrogen	Nickel	Silicon	Uranium
Calcium	Iodine	Nitrogen	Silver	Vanadium
Carbon	Iron	Oxygen	Sodium	Zinc
Chlorine	Lead	Phosphorus	Strontium	

Fig. 5–13. Variations in growth because of the addition of minerals to the soil. The plant is sweet clover; the soil was the same for all jars. There was a notable response to the addition of phosphorus and potassium (49) and a still greater response to phosphorus, nitrogen, and potassium (52). (Photograph, courtesy E. E. DeTurk, from *Hunger Signs in Crops.*)

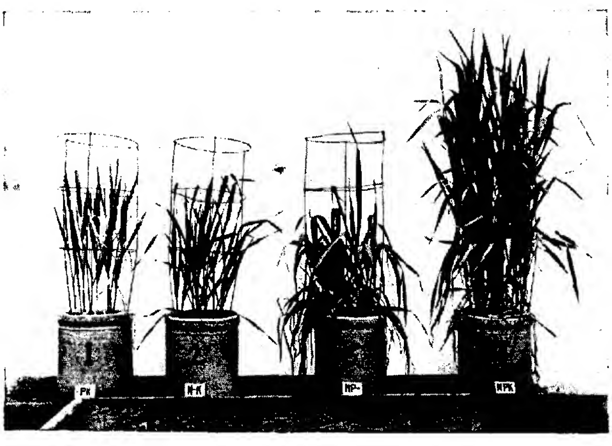


Fig. 5–14. Response of barley to the mineral elements, nitrogen, phosphorus, and potassium. Jar 4 received all three, the plants being healthy and vigorous; Jar 1 shows lack of nitrogen; Jar 2 lack of phosphorus; Jar 3 lack of potassium, plants having weak stems. (Photograph, courtesy George N. Hoffer, from *Hunger Signs in Crops.*)

The Entrance and Movement of Minerals

The mineral elements must enter the roots as salts dissolved in soil water. One of the physical processes involved in the absorption of minerals is diffusion, but many other complicated factors are involved. Diffusion is a physical process by which the molecules of a substance disperse. They may intermingle with those of another substance. One gas will diffuse into another. If a soluble substance is put into a solvent it will diffuse throughout the solvent. If we drop a crystal of some colored salt, such as copper sulphate, into a glass of water we can observe the diffusion by the color. The colored region, at first confined to the area about the crystal, continues to enlarge until finally the whole liquid becomes uniformly colored. The particles of the salt have moved from the place of their higher concentration to places of their lower concentration. In the end, the result is equal concentration throughout the whole solvent. The dispersal of material is brought about by molecular movement.

A crystal of a salt is a solid substance. Its molecules are held together by some force of mutual attraction. When a crystal is dropped into a liquid, such as water, the tendency of the molecules to hold together is reversed and replaced by a tendency to separate or spread as far apart as they can. The molecules may be separated into ultimate particles known as ions. The molecules and ions of a dissolved substance in a liquid are in constant motion and their mutually repellent movements cause them to diffuse from places of their greater to places of their lesser concentration. Certain types of membranes, when encountered, offer little or no resistance to the passage of substances dissolved in the water. However, the outer surface of the protoplasm, or plasma membrane, inhibits the free passage of some dissolved substances and therefore possesses to a greater or lesser extent the property of selective permeability. An important fact to keep in mind is that the permeability of the protoplasmic membrane is not constant but fluctuates with varying external and internal conditions. The root hair protoplasmic membranes in general permit the passage of many inorganic salts which are dissolved in the soil water. These salts move in the water by molecular diffusion. We must guard against thinking of their entrance by a movement of the water. The excess movement of solutes may be in one direction, while the excess movement of water is in the opposite direction. Temperature influences diffusion because it affects the rate of molecular activity.

Diffusion, however, is not the only process involved in the absorption of minerals. The life activity of the root hair cells—that is, their physio-

logical activity—probably plays an active part in absorption. If diffusion alone were involved, we should expect to find absorption of a particular mineral by a root hair only when its concentration was greater in the soil solution, since otherwise more of the mineral would be moving outward than inward. But we have reason to believe that a mineral can be absorbed even when there is more of it within the vacuole of the root hair than in the soil solution. The absorption of minerals is also affected by the acidity of the soil, by the presence of organic matter in the soil, by the general composition of the soil, and by other factors. This indicates that absorption of minerals is a physiological rather than a purely physical process.

Once the dissolved mineral substances reach the xylem they are conducted from the root to the leaves by the streaming, or mass movement of the water, in the dead tracheary elements. Their entrance into the living cells of the leaves involves the same physiological and physical processes as did their entrance into the root hairs.

THE CARBON AND NITROGEN SUPPLIES

In the synthesis of their foods green plants are constantly forming organic compounds in which carbon and nitrogen are bound. The available supply is not exhausted because there are means for releasing carbon and nitrogen from plant compounds and making them available for new syntheses. The courses followed by carbon and nitrogen are called cycles.

The Carbon Cycle

The utilization of the carbon dioxide gas of the air and water in the synthesis of carbohydrates by photosynthesis has been described in an earlier chapter. The entrance of carbon dioxide through the stomata and its movement through the intercellular spaces by diffusion also have been explained. When carbon dioxide is used in a cell in photosynthesis, its concentration within that cell is reduced; and, according to the laws of diffusion, more molecules will move into the cell than out of it, until the concentration is equalized. Through respiration, the carbon which is built into compounds by photosynthesis is returned to the atmosphere—the respiration of the plants themselves, respiration of animals which consume them, and respiration of the saprophytes which bring about decay after their death. Through combustion of plant and animal materials carbon dioxide is also released into the atmosphere. A diagrammatic representation of the circulation of carbon in nature is shown in Fig. 5-15.

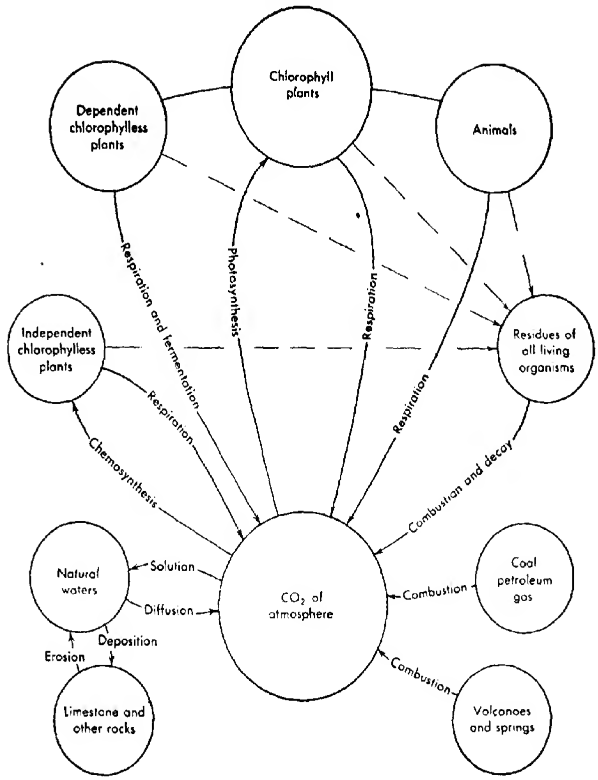


FIG. 5-15. The circulation of carbon dioxide in nature.

The Nitrogen Cycle

Nitrogen is essential for the synthesis of proteins and related compounds which are the principal constituents of protoplasm. Green plants obtain their nitrogen from nitrogenous compounds in the soil. The majority of plants absorb most of their nitrogen in the form of nitrates, although nitrites, ammonium salts, and organic nitrogen compounds may also be utilized. Nitrogen does not occur in the rocks from which soils are formed, and its presence in the soil is indicative of other sources. With the death of plants, or through the waste and death of animals, nitrogenous compounds reach the soil as organic residues. Saprophytic organisms, bacteria and fungi, decompose organic matter in the soil and in a series of reactions con-

vert it into ammonia, nitrites, and nitrates. Other bacteria add to the soil nitrogen supply by combining free nitrogen of the atmosphere with other elements to form organic nitrogenous compounds by a process known as nitrogen fixation. Fixation may be brought about by saprophytes which

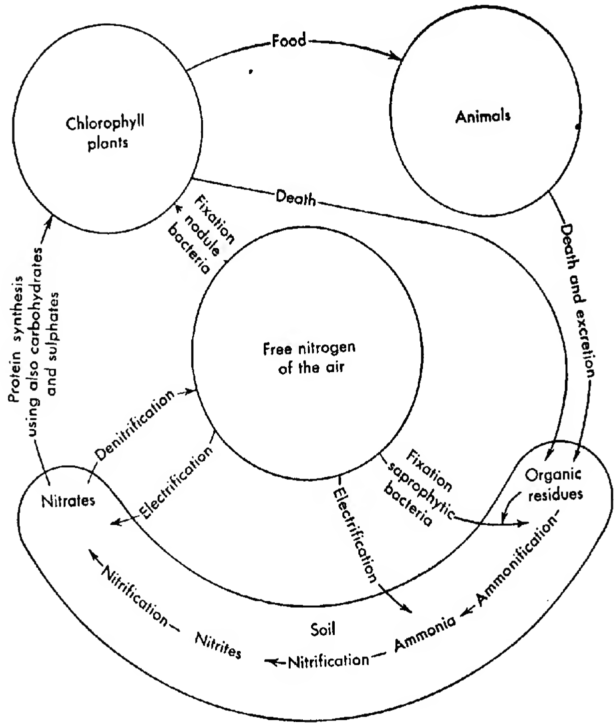


FIG. 5-16. The nitrogen cycle.

utilize dead organic matter, or by bacteria which live in nodules on the roots of members of the legume (pea) family. Indirectly, through the action of the nodule bacteria, atmospheric nitrogen is fixed and thus brought into the organic nitrogen cycle by legumes—clovers, alfalfa, peas, beans, vetches, and others. Some atmospheric nitrogen reaches the soil through rain water during electrical storms. Man has developed an artificial method of fixing atmospheric nitrogen by electrification. This has become of importance in the manufacture of commercial fertilizer. As the quantity of

nitrates in most soils is small, all means of increasing the supply are important. The complete relation of nitrogen to plant life involves a series of reactions some of which take place in the cells of soil organisms and some in the cells of the higher plants. A diagrammatic summary of the interrelations of the various events is presented in Fig. 5-16.

CHAPTER 6

REACTION OF PLANTS TO THEIR ENVIRONMENT

(Irritability, Adaptedness)

We have considered how plants manufacture food, how they obtain water and raw materials, how they derive energy, and how they build up their bodies. These are chemical and physical processes by virtue of which the life of an individual plant is maintained. These metabolic processes are primarily internal in nature but they are all more or less dependent upon external conditions. In order that the internal processes may proceed advantageously the vegetative parts must be favorably adjusted to their immediate surroundings. It must be evident that the external conditions and materials, such as heat, light, water, and salts, are not always uniformly distributed in the environment. If the separate leaves, stems, and roots could react so that they might adjust themselves to the most favorable positions, the advantage to the plant would be obvious. Fortunately for the plant, just such a capacity of reacting to external stimuli is inherent in it; it is called *irritability*. Plants not only possess such a property but manifest it to a high degree of efficiency. Our account would be incomplete indeed if we did not give consideration to the interesting and important phenomena which are included under this topic.

IRRITABILITY

Much of what is said here can be found in some presentations under the heading of *movements*. There is a reason why we may discuss the same things under the heading of *irritability* or of *movements*. Living things in adjusting themselves to the environment, i.e., in reacting to a stimulus, frequently give evidence of the response by movements. These may involve the organism as a whole or only parts of it. Of course, there are types of reactions other than movement which are not visible. We have chosen to direct attention to some of the stimuli which are responsible for causing plants to assume the positions they do, to point out how they react when

the conditions change, and to consider the ways in which the movements come about.

Response to Gravity

Ordinarily roots grow downward and shoots grow upward. Obviously this is advantageous because the roots are then in the soil where they can obtain water, and the shoots with their leaves are in the air where they are *in the light. But, as we shall see, it cannot be the water which effects the* downward growth of the roots, or the light which effects the upward growth of the green shoots.

As regards position we must be more specific in our statements. It is true that roots grow downward, but only the main or tap root assumes a vertical position. The branch roots assume a fairly definite angle with respect to the up-and-down axis of the main root. The same is true of stems. The main stem is vertical, the branches come off at an angle. The main axis of plants growing on a hillside is not at right angles to the surface of the ground but is vertical or upright. The branch roots and stems also show the usual angular relation to the main axis. In the search for an explanation of this situation even a brief consideration will suggest that the one force in nature which acts in up-and-down lines is gravity. We would seem justified in suspecting that gravitational force is the stimulus which is responsible for the positions taken by the roots and shoots. Much evidence can be had to confirm this hypothesis.

When a seed germinates, the young root emerges and turns downward and the stem turns upward regardless of the position of the seed. Even if the embryo in the seed is upside down the result is the same. The general term for such a response to a stimulus is *tropism*. The specific response to *gravity* is known as *geotropism*. Since the roots grow toward gravity they are said to show *positive geotropism*. Stems grow away from gravity and hence show *negative geotropism*. Lateral branches of either roots or stems growing at oblique angles or horizontally are said to show *diageotropism;* later branches growing in various directions and more or less disregarding gravity may be described as showing *plagiotropism*.

If we take a rapidly growing young seedling of some large seed, such as Windsor or scarlet runner beans, and place the tap root in a horizontal position, the root tip will turn downward. After a few hours the curvature will be complete and the tip will be pointing directly downward (Figs. 6–1, 6–2). Such an experiment may be set up by using a small box with a glass side. The box can be filled with damp sphagnum moss and the seedling can be placed close to the glass so that its position is readily observ-

able. Variations can be tried by arranging the straight tap root at various angles other than vertical. It is possible to record the original position by marks made on the outside of the glass with a wax pencil or with India ink and a fine brush. It will be observed that regardless of the original position the tip will be pointing downward after a few hours. Careful observation will reveal that the curvature is near the tip and that as the curvature has been brought about the root has been elongating. The elongation can be detected readily by the distance of the tip beyond the mark on the glass. But there is a still better way to check on the region of the curvature and

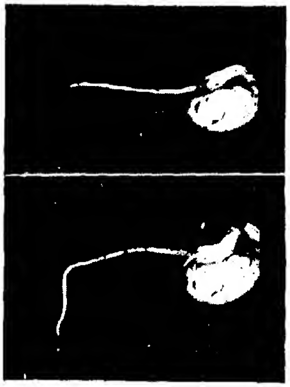


Fig. 6–1. Geotropism in young roots of bean seedlings; above, root placed horizontally; below, showing growth and curvature after a few hours.

its relation to the elongation. Small black dots of India ink can be placed equidistant (1 mm. is a good distance) on the white root before it is placed in position (Fig. 6–3). It will be found that the dots separate only in the region just back of the tip. It is in this region of elongation that the curvature has taken place.

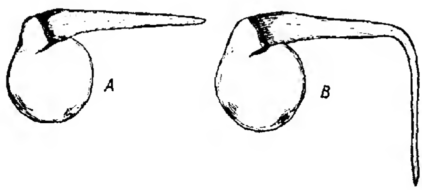


Fig. 6–2. Geotropism in roots of peas. *A*, root placed horizontally; *B*, the same root 24 hours later. (Drawing by F. Brown. Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

These observations should lead to the conclusion that curvature is correlated with growth. But we must inquire more particularly into the mechanism of the bending. We have concluded that growth is the motive force. But if the growth were of a normal or usual nature the tip would be pushed forward in a direct line with the axis of the root. But the growth is not of the usual sort when the root is placed in any position other than a vertical

one. There is then a differential growth, i.e., a more rapid growth on one side than the other. Since the root is stimulated to faster growth on the upper side than on the under side it is swung around so that its tip is directed downward.

In this connection there is another experiment which should be tried. If a straight tap root is placed in a horizontal position in such a way that it can be rotated slowly (this can be done with an instrument known as a clinostat which rotates by clockwork) there is no curvature; there is growth in a horizontal line. The revolving prevents the stimulus from acting on the root in a one-sided manner. If there is one revolution in about fifteen minutes all sides are equally exposed to the stimulus of gravity and we may say that the stimulus of gravity is neutralized so far as effecting a curvature is concerned.

It is possible to replace gravity with another force. We may continue to use our young seedlings for this experiment. By placing them on a

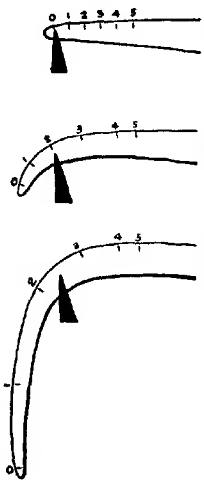


FIG. 6–3. Diagrams showing that geotropic curvature is in the region of elongation; further particulars given in the text. (After Sachs.)

rapidly rotating vertical disc, or wheel, it is found that the roots turn away from the center of the disc, and the shoots toward the center. In this arrangement the response is to centrifugal force and not to gravity. If the disc is revolving in a horizontal plane the force of gravity still operates and the result is an intermediate adjustment effected by the influence of centrifugal force and gravity combined. The actual position of plant parts is often the resultant of the effects of one or more stimuli.

Thus far we have centered our attention on the positive geotropism of roots. By choosing rapidly growing young stems negative geotropism may be observed and studied. For such studies potted plants may be used to advantage, and a comparison may be made with practically all the facts brought out in the root experiments. The stems turn upward, not in their lower nodes where elongation is complete but in the upper nodes where growth is still going on (Fig. 6–4). There is also a response on the part of the leaves brought about by bending of the petioles. If the plant is turned so that the main stem is in a horizontal position and is left in that posi-

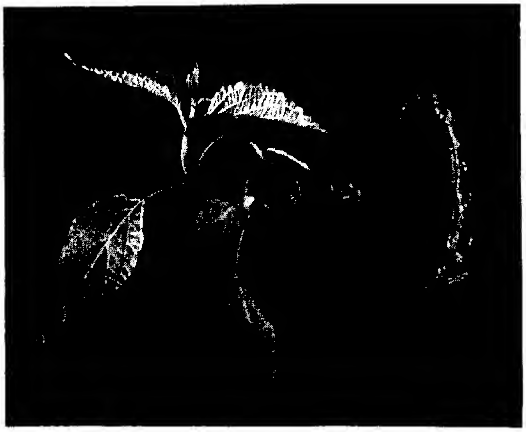


FIG. 6–4. Negative geotropism in stem of coleus which was placed in a horizontal position. (Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

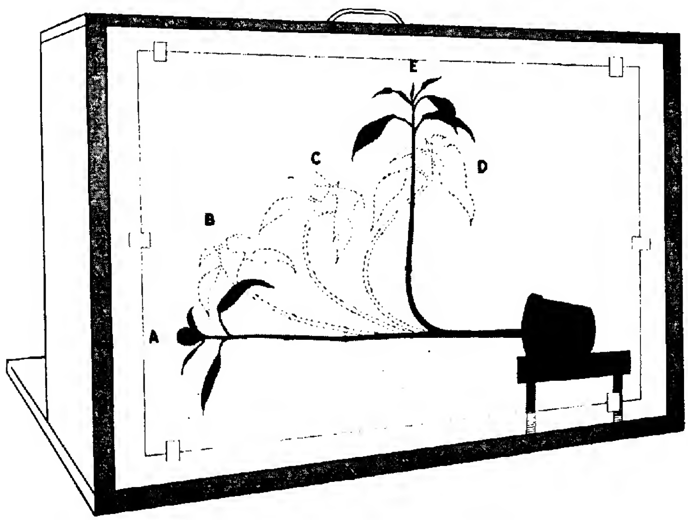


FIG. 6–5. Phases (*B–E*) of geotropic curvature in a shoot of *Impatiens* from horizontal position (*A*), shown by shadowgraph method described in text.

tion for several hours the curvature becomes complete and is evident at a glance. The change of position may be observed as it is going on, by arranging the plant so that it casts a shadow on a paper in such a manner that tracings of the shadow can be made (Fig. 6–5). With the aid of silhouettes

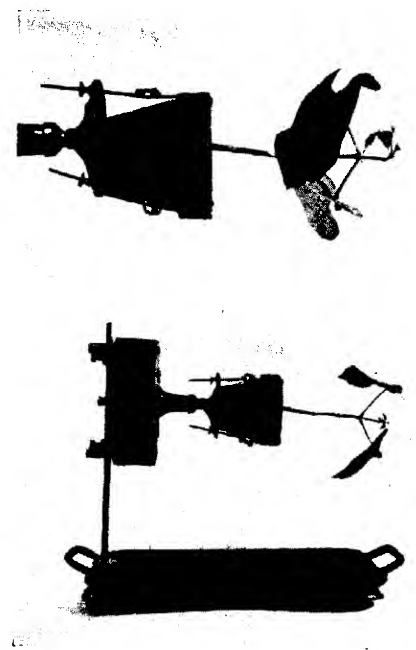


FIG. 6–6. A young bean plant in a horizontal position on a clinostat. There is no curvature below because of the rotation; above there is a curvature which took place after the rotation was discontinued.

it is possible to watch the gradual progress and to record how much takes place in a given interval. The rapidity of the reaction is generally a matter of surprise. If a shoot is placed in a horizontal position on a clinostat (Fig. 6–6) there is no curvature as long as the rotation is continued, but it takes place quickly if the rotation is stopped.

It is possible that the reader may wonder why we have not referred to the possibility that light is a factor in the upward growth of the shoot. Light does produce effects upon the growth of green shoots and hence must be discussed. But if we wish evidence that it is gravity and not light which

causes shoots to assume their upright position, we may obtain it by germinating seeds in the dark. We find that the shoots grow upward in the dark just as they do in the light (Fig. 6–7).

We have used the expression that the force of gravity is responsible for roots growing downward. But it must be understood that gravity does not

FIG. 6–7. Bean seedlings grow upright whether in light (left) or in the dark (right) (Photograph by L. O. Overholts.)

actually pull the roots downward. Gravity is also responsible for stems growing upward. Perhaps no one would think that gravity could push the stems upward because gravity is generally regarded as an attracting rather than a repelling force. We must think of gravity merely as a *stimulus*. The effect, or response, is produced by *growth*.

When a horizontally placed root or stem responds with a curvature it is believed to be due to an unequal distribution of auxin. Auxin moves downward and becomes more concentrated on the under side. Since higher concentration promotes growth in stems the increased growth on the lower side causes the stem to bend upward. Higher concentration apparently re-

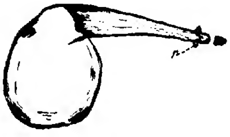


FIG. 6–8. The growing tip of a root has been removed; note failure to respond to gravity and the development of secondary roots (*r*). (Drawing by F. Brown. Reproduced by permission from *Botany* by Hill, Overholts, and Popp. Copyrighted 1936 by the McGraw-Hill Book Company, Inc.)

wards root growth and the greater growth on the upper side causes the root to bend downward. If the tip of a root is cut off there is no geotropic response (Fig. 6–8).

Our discussion has been confined thus far to the reactions of the higher plants to gravity. The simple vegetative parts of some of the lower plants would not seem to be subject to gravity, but if they grow flat on the ground and have distinct upper and lower sides (dorsiventral form) this is in itself a form of geotropic orientation. The fruiting branches of mosses and liverworts exhibit negative geotropism. The fructifications of many fungi show distinct geotropic responses. Ordinary mushrooms and toadstools are negatively geotropic, but many of the bracket fungi growing out of the sides of trees and logs form a definite angle with the downward direction of gravity and hence are diageotropic.

Response to Light

Much space has been devoted to geotropism. Gravity is the first stimulus to which a young plant is subjected and throughout the life of the plant it remains a predominant factor, but its influence is often modified by light. The growth response to light was formerly called *heliotropism,* but later workers have preferred the term *phototropism.*

Without doubt everyone is familiar with the fact that house plants placed near windows grow toward the light. The expression that plants "are drawn to the light" is sometimes heard. In these cases we are speaking of the stems and leaves. The stems and also the petioles show curvature, so that the leaf blades are more or less at right angles to the light from the window. It is interesting to compare a plant which has been grown in a greenhouse, where the light comes equally from all sides, with one grown in a window (Fig. 6–9). Even better than a window-grown plant is one grown in a dark chamber with only a small opening on one side.

On the greenhouse plant the main stem is upright; the branches, if any, radiate at fixed angles; and the leaves assume the positions determined by their origin from the stems. In this specimen it is evident that the type of plant and gravity have determined its form. In the specimen in one-sided illumination both gravity and light are influential and the final effect is a resultant of the reactions to these influences.

In the same way that we neutralized the effect of gravity by rotation we may neutralize the effect of light. By putting our plant on the clinostat all sides will be equally exposed to the light stimulus and no curvature results.

Study of a plant which has reacted to a one-sided source of light will

reveal that the curvature of the stem is in the upper internodes. It is certain that the response to light is brought about by growth and takes place only in the growing parts. In the older parts where elongation is complete there is no change of position. The positive phototropism of stems has usu-

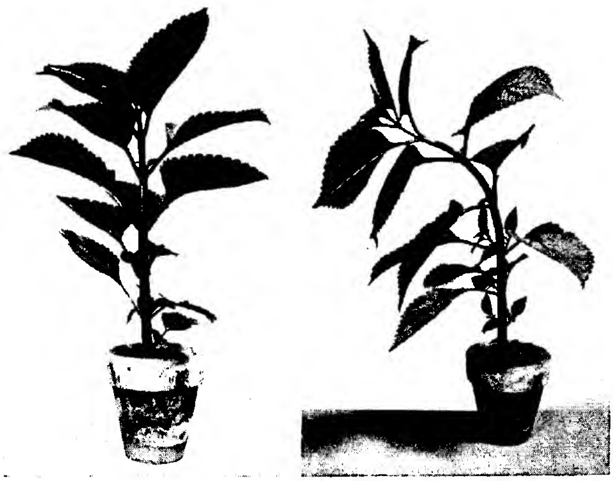


Fig. 6-9. A coleus plant which was kept in a uniformly lighted greenhouse (left) and then for several days in a chamber lighted only from one side.

ally been explained by the fact that light retards growth. Accordingly, the side of the stem toward the light would grow more slowly and the stem would curve toward the source of light because of the more rapid growth on the opposite side. It does not seem possible that such a simple hypothesis is sufficient to account for all the effects of phototropism. Mustard seedlings grown in water cultures and placed in a dark chamber which admits a beam of light from one side show a positive response of the shoot and a negative response of the root to the light stimulus. In the root the tissues grow faster on the lighted side, just reversing the situation in the stem. In both stems and roots the auxin moves away from the lighted side. Since this condition retards growth on that side in the stem and accelerates it in the root, the effects are opposite.

Some headway has been made in determining the region of perception of the light stimulus. It appears to be near the tips of parts, even though the region responding is farther back. For such studies Italian millet seed-

lings have been grown in the dark until they are about one inch high. Upon being exposed to one-sided illumination they bend at a rather sharp angle about 2/5 of an inch from the tip. This locates definitely the region of response. But if the tips are covered with tiny caps of tinfoil to a distance of 1/5 of an inch there is no response. From this it is concluded that the perceptive region is in the tip since there is no response when it is cov-

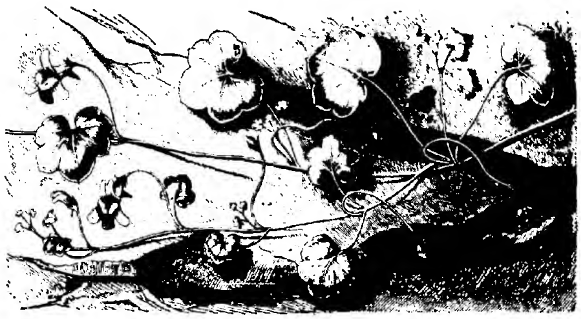


FIG. 6–10. Flower stalks of Kenilworth ivy, which bring the seed capsules into position for showing positive phototropism at first and a negative reaction later, dropping their seeds into clefts in the rocks. (After Kerner.)

ered even though the responding region is left exposed. There seems to be no doubt that a stimulus may be perceived in one location and the adjustment take place at another.

The phototropic sensitivity of organs may vary according to certain external influences or according to their internal stages of growth and development. The intensity of the light as well as the quality may be responsible for variations. Some plants in weak light react positively but will react negatively if the intensity of the light is excessive. Traces of coal gas as an impurity in the air affect phototropic responses. The flower stalks of Kenilworth ivy (*Linaria cymbalaria*) are at first positively phototropic, extending into the light and away from the rocks or walls upon which the plant is growing. After pollination they become negatively phototropic, elongating and turning backward. By this reversal the seeds are likely to be deposited in crevices or other favorable locations (Fig. 6–10).

It is generally accepted as a fact that many green plants do not need and cannot use all the energy of light that falls upon them in the summer. In some plants the position of the leaves becomes changed from a plane transverse to the more intense rays of midday to a plane more nearly parallel to these rays. There are two plants, one a wild lettuce (*Lactuca scari-*

ola) and the other a rosinweed (*Silphium laciniatum*), whose leaves in such an adjustment take more or less north and south directions and are commonly known as "compass plants" (Fig. 6–11). In contrast to such plants as these whose leaves show a permanent adjustment to the light rays are plants which exhibit temporary adjustments either between intense and diffuse light or between light and darkness. The leaflets of some plants fold together or take vertical positions in intense light and shift to horizontal positions in less intense light. Many plants of the legume (Pea) family—among them clover, peas, beans, senna, and acacia—fold their leaflets at night or in darkness. Such movements are commonly known as "sleep movements." They are responses to the stimulus of light, but the movement is not a growth reaction and so is not a tropism. The movement is accomplished by a change in the turgor pressure of the cells at the base of a leaflet and at the base of the petiole. They assume the usual positions in the light. In the so-called sensitive plant (*Mimosa pudica*) mechanical shock, as well as darkness, will bring about a folding of the leaflets and drooping of the leaves (Fig. 6–12). Some flowers close at night. It seems probable that temperature as well as light is influential. The opening and closing are accomplished by osmotic mechanisms and not by growth.

FIG. 6–11. Arrangement of leaves in a "compass plant," the one on the right showing the north and south adjustment. (After Kerner.)

In some plants where many leaves grow close together there is an obvious shifting of positions so that the leaf blades tend not to shade one another. Such an arrangement is accomplished by the bending and elongating of the petioles and may be observed on many trees. Good examples may be seen in wall climbers such as the various kinds of ivy. Such even placements of leaves have suggested the term *leaf mosaic* (Fig. 6–13).

There are certain responses to light which are included under the term *phototaxis*. Here belong the movements of free cells or of bodies such as chloroplasts within cells. There are some unicellular aquatic plants which

swim about by the aid of whip-like protoplasmic strands called flagella. There are also reproductive bodies such as zoospores of certain algae which are motile. In the dark such free-swimming bodies and cells frequently move about in all directions in an apparently aimless fashion. When illumi-

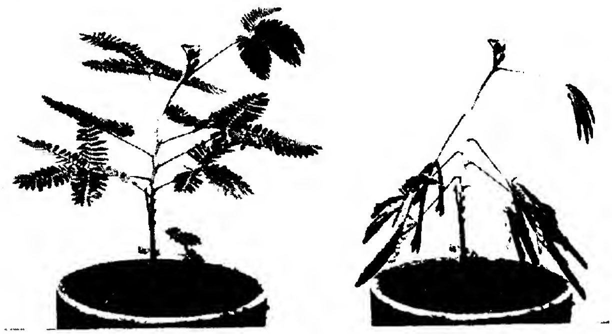


FIG. 6–12. The sensitive plant, *Mimosa pudica*. The folding of the leaflets and the drooping of the leaves as shown on the right may be brought about by mechanical shock or by darkness.

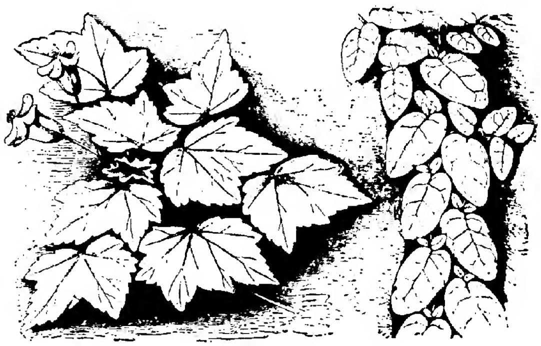


FIG. 6–13. Leaf mosaics, left a begonia, right a fig, both growing on a wall. (After Kerner.)

nated from one side only, a definiteness of direction is evident. They may move either toward the light or away from it. The advantage of zoospores of green algae reacting positively to the light is obvious since in this way they come to rest and establish themselves where the stationary adult will develop in the light. It is said that zoospores never come to rest if kept in

total darkness but keep on swimming continuously until exhausted. It should be added that other factors such as chemical substances and gravity affect free-swimming cells. Within cells chloroplasts are carried along passively by protoplasmic streaming, but they also move independently and arrange themselves within the cell in response to the conditions of light. They become oriented so that the broad surface is exposed to the rays of medium light and the edge toward the rays of intense light.

Response to Contact

The term applied to growth movements made in response to contact or touch is *thigmotropism*. The best example to consider is the case of tendrils. These are slender structures used by many climbing plants to secure themselves to a support. Tendrils move back and forth slowly until they come in contact with an object such as a stem or stake or wire, and then they make several turns around it. Proof that it is the contact with the support which acts as the stimulus can be obtained experimentally. Tapping the tendril on one side produces a turning and its progress can be observed. A quick contact will cause the tendril to bend, but it will straighten in case the contact is not continued. If the contact is maintained, a complete winding about the object results.

Anyone who has seen the prompt folding of the leaflets and drooping of the leaves of the sensitive plant when it is touched would be likely to think of it as a fine example of thigmotropism. On the contrary, the motor mechanism here is not growth but a change in the turgor pressure of certain cells (as we have already explained in connection with "sleep movements"). The result of a stimulus from a contact can be observed, as it travels along, by the successive closing of each pair of leaflets. Finally, when the impulse reaches the pulvinus (a swelling at the base of the petiole), the whole compound leaf droops. Sometimes a mere touch on the terminal leaflets is a sufficient shock. Intense heat applied momentarily by passing a burning match below the leaflets will act as a stimulus. A small drop of acid will also serve. A slight touch on the under side of the pulvinus will cause a sudden drooping of the leaf. After a time recovery ensues. The significance of these reactions is a mystery. They do not seem to be in any sense advantageous adjustments.

There are other reactions of plant parts to contact which do, however, have obvious advantages. Some insectivorous plants move in such a way as to capture insects which alight upon them. In the Venus's-flytrap the two halves of the leaves fold together quickly, thus catching and holding the insect. The contact is achieved by bristles on the upper surface of the leaves. In the sundew there are glandular hairs which secrete sticky drops that